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THE *ACANTHASTER* PHENOMENON

P.J. Moran

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The *Acanthaster* phenomenon

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PREFACE

This volume contains three works which were published separately over the last 2 years. The first of these was the scientific review "*The Acanthaster phenomenon*", which was published in *Oceanography and Marine Biology: an Annual Review*, during 1986 (Volume 24, pages 379-480). It is reproduced here with its original pagination with the permission of Aberdeen University Press. This review provided the basis from which the other two reports were derived. One was an annotated bibliography which contained full citations for the references given in the review as well as a number of additional references. This work was entitled "*Acanthaster planci: an annotated bibliography*" and was published as a technical report of the Crown-of-thorns Study (ISBN 0 642 11246 0) during 1986. In addition, a subject index to the review was compiled and published also as a technical report of the Crown-of-thorns Study. It was entitled "*The Acanthaster phenomenon: subject index*" and was produced in June 1987 (ISBN 0 642 11790 X). The page numbers given in the present subject index refer to the original pagination of the review.

Whilst the present volume is a compilation of these three works it is noteworthy in that it contains a second edition of the annotated bibliography which itself comprises a substantial number of additional references and an expanded list of annotations.

This volume reflects the hard work of a number of different people. Accordingly, I offer my most sincere thanks to Suzie Davies who painstakingly checked (and often corrected) all of the citations in the bibliography and to Jean Dartnall who produced the subject index to the review. I also wish to thank Alan Dartnall and Inara Bush for their encouragement and help in the production of this monograph.

Additional copies of this monograph can be obtained by writing to: The Librarian, Australian Institute of Marine Science, P.M.B. 3. Townsville MC. Queensland, Australia. 4810.

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THE *ACANTHASTER* PHENOMENON*

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INTRODUCTION

The crown-of-thorns starfish (*Acanthaster planci* Linnaeus 1758) has become one of the most well-known animals in coral reef ecosystems. This notoriety has developed not because of its beauty or its commercial value but because it forms large aggregations or outbreaks, which can lead to the destruction of extensive areas of coral. Over the last 20 years numerous observations and opinions have been recorded about this starfish. These have ranged from scientific papers and reviews on various aspects of the biology and ecology of this animal to discussions of its effects on the tourist industry. Most debate on this topic has addressed two main questions: first, what causes outbreaks and secondly, are they influenced by man's activities?

In the light of such debate this paper has several aims. First, to define the bounds of our current knowledge of *A. planci* by focusing on those aspects of the phenomenon that are best known. Secondly, to indicate areas of conflict and debate among scientists and to highlight anomalies in the available data. Thirdly, and of equal importance it is the aim of this review to define those aspects that are least known, but are important to our understanding of the phenomenon. Fourthly, it will highlight the inadequacies of the hypotheses at present put forward to explain the origin of outbreaks. Finally, the paper identifies the various problems confronting scientists in their attempts to understand a phenomenon that is large in scale, enormously complex, and exhibits interesting inconsistencies and synchronies.

Several small reviews exist reporting current research or particular aspects of the phenomenon (e.g. Talbot & Talbot, 1971; Caso, 1972; O'Gower, McMichael & Sale, 1973; Sale, Potts & Frankel, 1976; Rowe & Vail, 1984a,b) yet few major reviews (e.g. Endean, 1973b, 1976) have been undertaken on this topic. The most recent (Potts, 1981) covered all research conducted until 1978. Since then a further series of outbreaks has occurred in various parts of the Indo-Pacific region leading to a resurgence in research and the development of several new ideas concerning outbreaks and their possible causes. These events have provided a justification for presenting this review as well as the desire to report this new information in

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the context of past results and hypotheses. Wherever possible the terminology in this paper follows that used by Potts (1981) who made a conscious attempt to avoid emotive terms, such as plague and infestation, because of their association with events that are somehow considered to be unpleasant, disastrous, and often unnatural. Consequently, the less emotional term, outbreak, has been used to describe large aggregated populations of starfish in this paper.

In essence, the *Acanthaster* phenomenon is a predator-prey interaction where the predator, *A. planci*, feeds on its prey, the corals. The two are intimately linked and should not be studied in isolation. Both must be investigated in order to comprehend fully the phenomenon, as the abundance of one changes in response to the abundance of the other (Bradbury, Hammond, Moran & Reichelt, 1985). Such dynamics are most readily seen in the interactions observed in various terrestrial ecosystems such as that between the lynx and snowshoe hare in Canada (Tanner, 1975). From a scientific viewpoint the occurrence of outbreaks of *A. planci* are unusual as this animal is a carnivore. Most references to outbreaks in the literature commonly involve herbivores such as locusts and other pest species (e.g. Ricklefs, 1979) and even sea urchins (North & Pearse, 1970). It is rare that a carnivore outbreaks on its own and that such outbreaks are not linked to increases in the abundance of its prey. There are even fewer reports of starfish outbreaking in the field. A notable exception is *Asterias forbesi* which has been recorded to outbreak in oyster grounds in the United States (Kenny, 1969).

Scientifically, outbreaks of *Acanthaster planci* are interesting as they provide an excellent opportunity first, to address certain key questions relating to the regulation of populations and secondly, to understand more about the dynamics of coral reef systems. Potts (1981) lamented the fact that ecologists had failed to use this natural experiment to their advantage. Perturbations on this scale offer scientists the opportunity to gain a deeper insight into the processes involved in structuring reefal systems as the systems themselves alter in response to the disturbance. While the results gained from studies of *A. planci* may have broad ramifications in several areas of marine ecology they may have importance in other scientific fields. For example, to date it has been used for testing neuropharmacological drugs (Buznikov, Malchenko, Turpaev & Tien, 1982), for synthesizing corticosteroids (Sheikh & Djerassi, 1973) and for investigating the physiological properties of echinoderm tissues (Motokawa, 1982).

THE ACANTHASTER DEBATE

The debate surrounding the *Acanthaster* phenomenon has developed into a very complex and emotional issue as the outbreaks themselves have involved people from many different parts of society and have affected the livelihoods of many people (e.g. those associated with the tourist industry). As a result, debates concerning the cause of outbreaks have involved a mass of opinions ranging from emotional calls for action to be undertaken (an understandable feeling if the effects of a large outbreak have been observed at first hand), through to informed and un-informed viewpoints from

politicians and the general public. Enmeshed within these views and often swamped by them are those of the scientists. Like the public, their opinions also have varied since they have not been immune from the emotional aspects of the debate (*e.g.* Dwyer, 1971; Endean, 1971b; Hazell, 1971; Talbot, 1971; O'Gower, Bennett & McMichael, 1972; O'Gower, McMichael & Sale, 1973; Bradbury, 1976; Bradbury, Done *et al.*, 1985; Rowe & Vail, 1985). Kenchington (1978) has given a thorough account of the various forces (*e.g.* scientific, historical, sociological, political, and economic) which were responsible for the controversy that surrounded the occurrence of outbreaks in Australia during the 1960s and 1970s. It would appear that in some instances the outbreaks were all but forgotten in the rush to enter the debate.

In some ways, scientists have only themselves to blame for the turmoil which has developed from this issue. When outbreaks were first reported (at a time when very little was known about them) numerous dire predictions were made by members of the scientific community. Some warned that outbreaks of starfish might lead to the mass erosion of reefs in the Indo-Pacific region which in turn might expose previously protected coastlines to erosional forces (Chesher, 1969a; Weber, 1970; Antonius, 1971). Others predicted that outbreaks would result in the destruction of the fishing industry and the loss of tourism (Chesher, 1969a; Vine, 1972). In addition, it was suggested that they may cause an increase in ciguatera poisoning (an algal-derived toxin in edible fish) since outbreaks produced large areas of substratum dominated by algae (Barnes, 1966) (see p. 441). To date, none of these predictions has been confirmed. This has led to a certain ambivalence on the public's part, towards the opinions and views of scientists (Raymond, 1984).

Since the early 1970s a number of committees of inquiry have been established to investigate the *Acanthaster* phenomenon and many of these have taken place in Australia. The first two committees formed (by the Federal and Queensland Governments) in this country (Walsh *et al.*, 1970, 1971) reported on what was known about *A. planci* at that time and sought to ascertain whether the starfish constituted a threat to the Great Barrier Reef. They also determined whether control measures should and could be implemented. Both committees recommended that extensive research be carried out on the phenomenon although the second committee concluded, on the basis of its findings, that *A. planci* did not "constitute a threat to the Great Barrier Reef as a whole" (Walsh *et al.*, 1971: p. 6). The conclusions of that committee, particularly the one just mentioned, were challenged and debated (*e.g.* Dwyer, 1971; Endean, 1971b; Talbot, 1971; O'Gower *et al.*, 1972; James, 1976). During 1971 an advisory committee was established to implement the policies of the second committee of inquiry and to co-ordinate future research. Over the ensuing years many aspects of the biology of *A. planci* were studied. The progress of these studies was reported in a document prepared by the advisory committee (Walsh, Harvey, Maxwell & Thomson, 1976) and in it further research was recommended particularly on the ecology and population dynamics of the starfish and its coral prey. With the decline of starfish outbreaks during the latter half of the 1970s research on *A. planci* waned. A further committee was established (by the Great Barrier Reef Marine Park Authority) not long

after a second outbreak was reported at Green Island at the end of 1979. Once again the results of previous research were reviewed and the significance of those outbreaks was assessed to determine whether further research was warranted. That committee considered the situation serious enough to recommend that several types of research be undertaken, addressing a number of broad aspects of the phenomenon (Advisory Committee on the Crown of Thorns Starfish, 1980). Some of this research was implemented although field studies on the ecology of the starfish were largely neglected. In view of the seriousness of the current series of outbreaks on the Great Barrier Reef another committee was formed with similar aims to those preceding it (Crown of Thorns Starfish Advisory Committee, 1985). In contrast to the findings of the second committee of inquiry this committee concluded that "the destruction of hard coral by aggregations of *A. planci* poses a serious threat to the organisation and functional relationships within some reef communities within the Great Barrier Reef, at least in the short term" (*loc. cit.*, p. 1). It also recognized that outbreaks of starfish posed a "major management problem in some areas of the Great Barrier Reef" (*loc. cit.*, p. 1). On the basis of its findings the committee recommended that a co-ordinated programme of research be conducted over five years at an estimated cost of \$A 3 million. Despite the reviews of these committees and the impetus that they gave to research they have not managed to quell the questions and debates, in Australia at least, concerning the phenomenon.

Frequently the debate surrounding the occurrence of outbreaks has been reduced to whether they are seen to be a problem, or threat to the reef and, ultimately, whether they are natural or man-induced events. Logic would have it that if they are natural then nothing is required except to adopt sensible management in areas of commercial interest. If unnatural then action may be required. Reducing the debate to this simplistic level at this time is trivial, as our knowledge of the phenomenon is inadequate to make rational decisions even in regard to these questions. All opinions, even those of scientists intimately associated with the phenomenon, are based to varying degrees on inadequate information. In conclusion, it is more realistic to suggest that outbreaks are a problem not because they may be natural or unnatural but because so little is known about them.

GENERAL BIOLOGY OF *A. PLANCI*

INTRODUCTION

Perhaps more is known about the general biology of *A. planci* than any other aspect of this animal. Research since the late 1960s has tended to concentrate on biological aspects; first, in order to gain a better understanding of the animal and secondly, as a means of establishing a store of knowledge upon which future experimentation may be based. Much of this research has been carried out in the laboratory (Potts, 1981) and has involved studies in the following five general areas: morphology, systematics, life history, growth, feeding and movement of *A. planci*. While these studies have increased our knowledge of *A. planci* they also have caused further controversy as some laboratory results have been found to be inconsistent

with those obtained from field studies (these inconsistencies will be discussed in the following sections). The validity of results from laboratory studies has been questioned as they are derived under conditions which may be more artificial and simplistic than those found in the field. Even though this criticism may be justified care also should be undertaken when interpreting the significance of results from field studies as very little is known about the ecology and dynamics of *A. planci* populations. It should also be borne in mind that the results from field studies may not reflect the effects of the variable being tested, but a complex of variables which are poorly understood.

MORPHOLOGY

A. planci (Fig. 1) is a carnivorous starfish found on reefs throughout the Indo-Pacific region. A detailed description of the external features of this animal has been given by Caso (1970). It is a large asteroid which may grow to more than 700 mm in diameter (from arm tip to arm tip) in the wild (see Lucas, 1984). Measurements conducted throughout the world have shown that adults normally range in size from 250–350 mm (Campbell & Ormond, 1970; Nishihira & Yamazato, 1972; Cheney, 1974; Ormond & Campbell, 1974; Kenchington, 1977).

A. planci is multi-coloured and individuals have been reported to range from purplish blue with red-tipped spines (Clark, 1921) to green with yellow-tipped spines (Branham, 1973). The general colour of an individual, which depends on the degree of extension of the dermal papulae (Clark, 1921), may vary through time (Barnes & Endean, 1964; Barham, Gowdy &

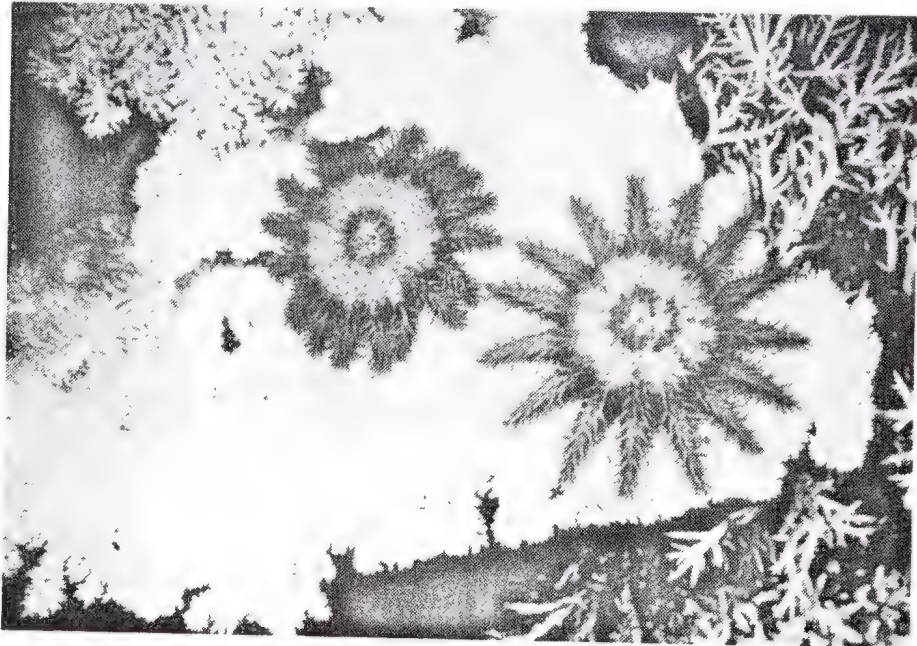


Fig. 1.—The crown-of-thorns starfish (*Acanthaster planci*) seen on recently dead (white) coral.

Wolfson, 1973). This variation is thought to be related to the effects of diet (Branham, 1973).

Adults generally possess from 8–21 arms or rays, although this figure has been found to vary from place to place (Table I). A number of small rounded plates known as madreporites are situated on the aboral surface of the oral disc. Their relative position has been used, in conjunction with other variables, to identify individual starfish (p. 421). Adult *A. planci* may have between 3 and 16 madreporites (Hyman, 1955; Caso, 1970; Barham *et al.*, 1973; Glynn, 1982b). Adults have also been found to possess from 1–6 anuses (Glynn, 1982b).

TABLE I

Variation in the number of arms or rays of adult starfish from different areas of the Indo-Pacific region

Area	No. of arms	Reference
Great Barrier Reef	14–17	Endean, 1969
Guam	14–18	Cheney, 1974
Gulf of California	12–15	Barham <i>et al.</i> , 1973
Gulf of Thailand	8–17	Piyakarnchana, 1982
Indonesia	10–18	Aziz & Sukarno, 1977
Okinawa	11–21	Nishihira & Yamazato, 1972
Red Sea	13–15	Ormond & Campbell, 1971

The exterior of *A. planci* is covered by numerous spines up to 40–50 mm in length (Endean, 1973b) which may grow at a rate of 1.3 mm per month (Pearson & Endean, 1969). Caso (1970) identified six types of spines on the aboral and oral surfaces of *A. planci* (lateral, marginal, ventral, adambulacral, ambulacral, and buccal). Recently, Walbran (1984) compiled an atlas of the most common skeletal components of this starfish. This included a discussion on the morphology, micro-structure, and architecture of preserved fragments as well as those found in sediments. A comparison was also made between these skeletal components and those from other starfish commonly occurring on the Great Barrier Reef. Walbran (1984) concluded that the skeletal components of *A. planci* (even those found in sediments) could be differentiated readily from those of other starfish on the basis of morphology, colour, and micro-structure.

TOXICITY

Apart from being abundant and structurally diverse the spines of *A. planci* can inflict a toxic reaction. As well as inflicting a painful wound they may cause several other symptoms including nausea, vomiting, and swelling in humans (Barnes & Endean, 1964; Pope, 1964; Weber, 1969; Odom & Fischermann, 1972; Williamson, 1985). No evidence has been found to indicate that a venom is actively injected into the wound created by a spine (Fleming, Howden & Salathe, 1972). Toxic compounds have been isolated from the spines of *A. planci* by Croft, Fleming & Howden (1971) and Taira, Tanahara & Funatsu (1975). The substance isolated by Croft *et al.* (1971)

was found to be a saponin which was present in the tissue overlying the spines. It was thought that this compound was present in insufficient quantities to cause the toxic reactions normally associated with this starfish (Croft *et al.*, 1971). At present it is not known what causes these reactions which are sometimes severe. Crude extracts of material isolated from the surface of spines have been found to have a haemolytic effect on human red blood cells (Everitt & Jurevics, 1973). Biochemical studies by Heiskanen, Jurevics & Everitt (1973) have indicated that inflammation around the wound may be mediated by the activities of histamine-like compounds whereas the pain associated with being pierced by a spine may be due to another cause.

Because they are abundant, large, and toxic the spines of *A. planci* are thought to represent a specialized adaptation which serves to protect the animal from predation (Cameron, 1977; Moore, 1978). This may be true but it is not known to what extent they prevent predation nor is it known how toxic they are to other marine animals. Indeed, very little is known about the quantitative aspects of predation of this starfish (see pp. 414-418).

HABITAT

Studies of the distribution of *A. planci* on reefs have shown that it prefers to live in sheltered environments such as lagoons and also in deeper water on the windward slopes of reefs (Chesher, 1969a; Pearson & Endean, 1969; Ormond & Campbell, 1974; Moran, Brabury & Reichelt, 1985). In general, this starfish avoids shallow or exposed locations where it is susceptible to wave action. Aggregations of starfish have been recorded to depths of 30 m (Branham, Reed, Bailey & Caperon, 1971) while individual starfish have been observed at approximately 40 m (Devaney & Randall, 1973). It is likely that they inhabit greater depths as an *A. planci* was dredged from almost 64 m near Euston Reef in the Great Barrier Reef (Great Barrier Reef Marine Park Authority, unpubl. data). An unconfirmed report exists of a starfish being found off Hawaii at a depth of 100 m (Chesher, 1969a).

SYSTEMATICS

A. planci has been known for many years. It was first described by Rumphius in 1705 and later by Plancus and Gualtieri in 1743 (Vine, 1973) and named in 1758 by Linnaeus. An historical account of the early description and classification of *A. planci* has been given by several authors (Weber, 1969; Branham, 1973; Vine 1973). There continues to be confusion as to the number of valid species referable to the genus *Acanthaster*. Madsen (1955), in reviewing the genus recognized two distinct species, *A. planci* and *A. ellisii*, the latter being found only in the eastern Pacific region. A third species, *A. brevispinus*, which at that time was known only from the Philippines was proposed. Its status, however, as a separate species was thought to be doubtful. Caso (1961) considered *A. ellisii* to be a valid species and divided it into two subspecies, *A. e. ellisii* and *A. e. pseudoplanci*. Barham *et al.* (1973) also argued for the separation of *A.*

ellisii from *A. planci* on the basis of its different behavioural characteristics; tending not to be cryptic during daylight hours, and appearing not to aggregate or migrate. They also pointed out that the disc diameter/arm length ratio for this species is different from that of *A. planci*. These distinguishing features have, however, been regarded by Glynn (1974, 1976) as being minor and reflecting the normal range of variability present in *A. planci*.

Attempts were made by Lucas & Jones (1976) to evaluate the status of *A. planci* and *A. brevispinus* by crossing individuals from an area of neighbouring sympatry on the Great Barrier Reef. Although both species were shown to have a high degree of genetic compatibility they were regarded as sibling species. Lucas & Jones (1976) argued that hybrids did not occur naturally on the Great Barrier Reef as ecological barriers prevented the exchange of genetic information between the two species. Unlike *A. planci*, on the Great Barrier Reef *A. brevispinus* is not found on reefs but occurs in deep water between reefs. Also it does not feed on corals but is thought to be an omnivore, preferring a more general diet. The results from recent studies have substantiated the claim that there is no exchange of genes between these species. Lucas, Nash & Nishida (1985) have demonstrated that larvae from F2 and hybrid x parental crosses are of low viability and suffer a high rate of developmental abnormalities. Furthermore, while the two species share common alleles for most gene loci they are homozygous for different alleles at one presumptive locus. From this biochemical genetic evidence they concluded that *A. planci* had evolved recently from a more generalist ancestor similar to *A. brevispinus*.

While there is good evidence to support the separation of *A. planci* and *A. brevispinus*, the taxonomic status of *A. ellisii* remains uncertain. A biochemical genetic study has indicated that this species is very similar to *A. planci* (Lucas *et al.*, 1985). At present gene frequencies for *A. ellisii* and *A. brevispinus* exist only for a single population of each ($n = 53$ and 11, respectively) and nothing is known of their variation between populations. The only information on this topic for *A. planci* comes from studies conducted by Nash (1983) who analysed seven populations within a large area, from Lizard Island to One Tree Island (Capricorn-Bunker Group: see Fig. 7, p. 431), on the Great Barrier Reef. He found that the genetic composition of starfish populations over this region was generally homogeneous. A population at Green Island was found to be genetically different from the others but the reasons for this were unable to be established.

Taxonomic uncertainty has occurred at the family level as well as the species level. The two species *A. planci* and *A. brevispinus* form part of the monogeneric family Acanthasteridae which was recently aligned with the family Oreasteridae on the basis of certain skeletal characteristics (Blake, 1979). In doing so the family was assigned from the order Spinulosida to the order Valvatida. This alteration is at variance with the findings of Mochizuki & Hori (1980) who suggested on the basis of immunological and morphological evidence, that a close affinity existed between the families Acanthasteridae (*A. planci*), Solasteridae and Asterinidae, all of which occur in the order Spinulosida. A close affinity was also proposed between these families and the Ophidiasteridae in the order Valvatida.

There is very little fossil evidence to support theorized phylogenies within

the genus *Acanthaster*. A possible relative of this genus may extend back to the Cenozoic period, but this conclusion is based on incomplete fossil evidence (Blake, 1979).

REPRODUCTION AND LIFE CYCLE

A. planci is a gonochoristic (dioecious) species which reproduces sexually. Unlike some starfish (*e.g.* *Linckia* spp.) it is not known to reproduce asexually by arm autotomy or somatic fission (Yamaguchi, 1975b). Studies in the field have found that the ratio of males to females is almost one to one (Pearson & Endean, 1969; Nishihira & Yamazato, 1974). Like many other invertebrates, planktonic larvae of *Acanthaster planci* are produced by external fertilization. Estimates have been made of the number of eggs that may be spawned by a single female during one season. Pearson & Endean (1969) calculated that females may contain from 12–24 million eggs. Recently, Conand (1983) suggested that large individuals (400 mm diameter) may produce as many as 60 million eggs during one season.

There is still some uncertainty regarding the timing and duration of the spawning season of *A. planci*. On the Great Barrier Reef spawning has been reported between December and January when the water temperature is above 28 °C (Pearson & Endean, 1969; Lucas, 1973). Reports from other areas in the Indo-Pacific region, indicate that it may vary according to location (Table II). In addition, while spawning in some areas is relatively restricted, occurring over a few months of the year (*e.g.* Great Barrier Reef), there are places where it seems to be more prolonged occurring intermittently over a number of months (*e.g.* Gulf of California). Indeed, in some areas fertile eggs have been collected from starfish throughout the year (Branham *et al.*, 1971; Yamazato & Kiyan, 1973) suggesting that there is an almost year-round potential for spawning. This potential has been

TABLE II
Spawning period of A. planci reported for different locations in the Indo-Pacific region

Location	Spawning period	Reference
Fiji	Dec. Feb.	Owens, 1971
Great Barrier Reef	Dec.-Jan.	Pearson & Endean, 1969; Lucas, 1973
Guam	Nov-Dec.	Chesher, 1969a
Gulf of California	Sept. Oct.	Cheney, 1974
Hawaii	Apr.-	Dana & Wolfson, 1970
Java	Apr. May	Branham <i>et al.</i> , 1971
New Caledonia	Apr.-	Mortensen, 1931
Okinawa	Nov. Feb.	Conand, 1983
Panama	June-July	Yamazato & Kiyan, 1973
Red Sea	Jan.	Glynn, 1974
Western Australia	July-Aug.	Roads & Ormond, 1971
Western Samoa	Nov.-Jan.	Wilson & Marsh, 1975
	Dec. Jan.	Garlovsky & Bergquist, 1970

demonstrated also for the Great Barrier Reef but there is no evidence of this actually occurring (Lucas, 1973). While there is the potential for prolonged spawning it would appear that this is not a significant occurrence and that spawning normally takes place within a well-defined period of a few months. The data presented in Table II indicate that spawning is concentrated between May and August in the Northern Hemisphere and November to February in the Southern Hemisphere. A similar breeding season for areas north of the equator was proposed by Birkeland (1982). Yamazato & Kiyan (1973) have argued that the spawning period for *A. planci* is more extended in the tropics than in the higher latitudes as those areas experience longer periods of high water temperature.

Apart from geographical variations in the timing and duration of the spawning period of *A. planci* it has been reported also that spawning in some areas is variable from year to year (Wilson & Marsh, 1975). These variations may reflect local changes in environmental factors such as temperature (Cheney, 1974) which is important in influencing spawning (Cheney, 1972a; Lucas, 1984). In addition, they may reflect the different methods (gonad index, gonad dissection, gonad histology) used to determine the reproductive state of starfish (Lucas, 1972). Additional variability in these determinations may occur as gonad size and state has been found to vary widely in isolated *A. planci* yet remain uniform in aggregated individuals (Cheney, 1974).

There have been several reports of *A. planci* spawning in the field. Owens (1971) and Branham *et al.* (1971) observed spawning starfish in Fiji and Hawaii, respectively. Perhaps the best account of this phenomenon is that given by Pearson & Endean (1969) who described a spawning event on the Great Barrier Reef. In particular, they noted the behaviour of starfish before, and during the release of gametes which lasted for approximately 30 min in both sexes (Fig. 2). Although most were males, one female was seen to spawn in their vicinity. Spawning has been reported in the laboratory by Branham *et al.* (1971) and Misaki (1974, 1979). Lucas (1984) also reported that a group of hybrids spawned in his aquaria during winter. Spawning can be induced artificially by injecting ripe adults with a prepared solution of 1-methyladenine (Yamaguchi, 1973b) provided the starfish are in the final stages of gametogenesis.

A substance has been isolated from the gonads of both male and female starfish which is thought to synchronize the release of gametes by starfish (Beach, Hanscomb & Ormond, 1975). Similar amounts of this compound were found in both sexes and neither showed a contrasting sensitivity to it. Experiments conducted in the laboratory have demonstrated that this substance is released during spawning and that once released it induces nearby starfish to spawn. In addition, its release stimulated the movement of starfish in the direction of the spawning individual. Apart from the limited observations of Pearson & Endean (1969) there are very few eyewitness accounts of synchronized spawning. The results of Beach *et al.* (1975), however, suggest that this pheromone-like compound may be an important factor in determining the numbers of larvae produced during a spawning period since it has the potential to induce starfish to aggregate and spawn synchronously. No experiments have been conducted in the field to determine whether the degree of fertilization of eggs is positively correlated with adult density. Lucas (1975) considered that normal, non-aggregated,

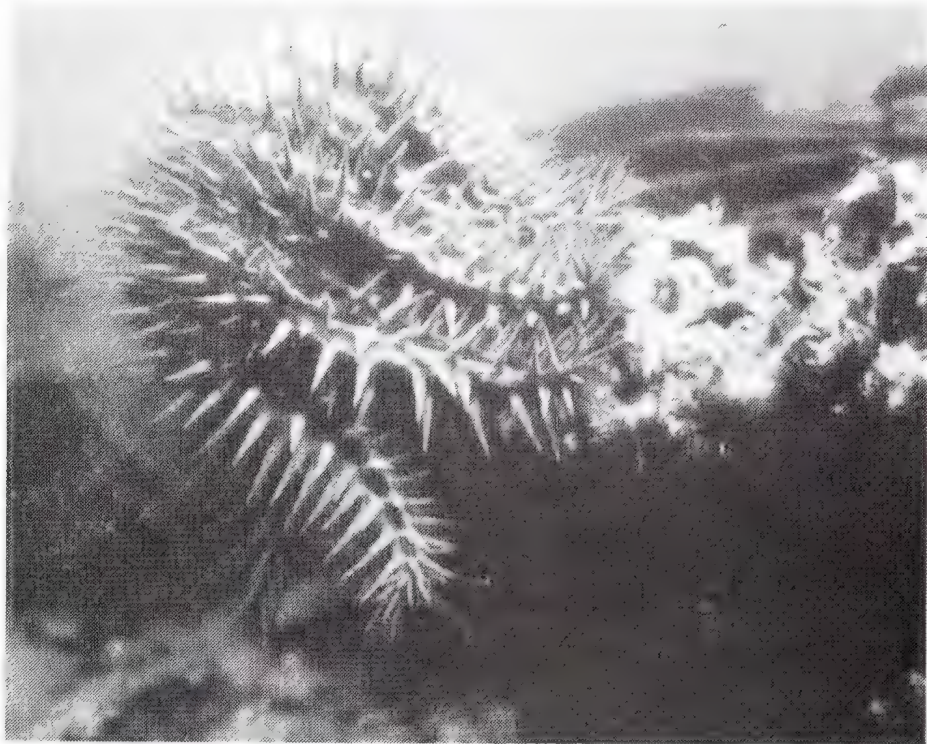


Fig. 2.—Typical behaviour of a spawning adult (photograph taken by J. Davidson).

populations of *A. planci* were likely to produce few larvae as such adult densities would not lead to a high rate of fertilization.

Information on the life cycle of *A. planci* has come mainly from studies conducted in the laboratory (Potts, 1981). Six main stages have been identified and they are summarized in Table III. The last four stages were described by Lucas (1984) from laboratory studies. The general life cycle of this starfish is presented diagrammatically in Figure 3. Once fertilized, the egg of *A. planci* develops from an embryo into a larva which feeds on phytoplankton (Henderson & Lucas, 1971). During its planktonic life, which may be up to a month in duration (Yamaguchi, 1972a, 1973b), it passes through several developmental phases after which time it settles and metamorphoses into a five-armed juvenile. The last process takes about two days (Henderson & Lucas, 1971). Initially, this juvenile starfish is thought to eat mostly encrusting and epiphytic algae and its growth rate is relatively slow. After approximately six months it has the morphology of an adult and changes its diet to corals. Although the growth rate of this starfish is high during this period it is not capable of reproducing and hence it is termed a coral-feeding juvenile. The general term juvenile (*e.g.* Laxton, 1974) is often applied to starfish belonging to either of the first two post-metamorphic categories delineated by Lucas (1984). According to laboratory growth studies *A. planci* begins reproducing towards the end of its second year (Lucas & Jones, 1976) and is then referred to as a coral-feeding adult. Lucas (1984) found that the growth rate of starfish during this stage

TABLE III
Stages in the life cycle of *A. planci* (after Lucas, 1984): *age from metamorphosis

No.	Stage	Age	Size (mm)	Growth rate	Food	Feeding rate	Fecundity
i	Laval	0-28 days	0.1-1.2	—	Unicellular algae	—	—
ii	Settlement/Meta-morphosis	0-2 days	0.3-0.5	—	—	—	—
iii	Algal feeding juvenile	0-6 months*	1-10	Low (exponential)	Encrusting and epiphytic algae	—	No
iv	Coral feeding juvenile	6 months-2 yr*	10-200	High (von Bertalanffy)	Coral	High	No
v	Coral feeding adult	2-3 yr*	200-350	Decreasing	Coral	Decreasing	High
vi	Senile adult	>3 yr*	350	Low	Coral	Low	Low

after which time the starfish are likely to die (Lucas, 1984). Several inconsistencies in the biological data presented for the phases identified by Lucas (1984) will be discussed in a later section (see pp. 393–397).

LARVAL BIOLOGY

Lucas (1982) recognized seven distinct stages in the development of larvae some of which are shown in Figure 3. This process began with the hatching of the embryo as a gastrula larva and proceeded through the following six stages; early bipinnaria, advanced bipinnaria, early brachiolaria, mid brachiolaria, late brachiolaria, settlement and metamorphosis. Prior to the commencement of this process, the eggs when shed by the female are approximately 0.2 mm in size, light yellow in colour (Henderson & Lucas, 1971; Yamaguchi, 1973b, 1977) and are negatively buoyant (R. Olson, pers. comm.). The sperm are much smaller and possess a spherical head (0.002 mm in diameter), middle section and long (0.04–0.05 mm) flagellum (Henderson, 1969). After fertilization, the embryo develops to the blastula stage (which has a wrinkled exterior) within seven hours (Hayashi, Komatsu & Oruro, 1973) and hatches as a free-swimming gastrula after about 30 hours (Henderson, 1969). It then develops into a bipinnaria larva and begins feeding on unicellular algae. Development to the bipinnaria stage may take from two to four days (Yamaguchi, 1977; Henderson, 1969).

Mortensen (1931) was the first to rear larvae to the brachiolaria stage in the laboratory. Other early larval studies were unsuccessful. Henderson (1969), Branham *et al.* (1971), and Henderson & Lucas (1971) reared larvae in the laboratory to the juvenile starfish stage. These studies demonstrated that the rate of development of larvae to the brachiolaria stage may be affected greatly by small changes in temperature. The time taken for larvae to develop to the brachiolaria stage has been variously reported to take from 9 days (Lucas, 1982) to 12 days (using normal sea water that was high in phytoplankton) (Yamaguchi, 1977) at 28 °C, 16 days at 27 °C (Mortensen, 1931), and 23 days at temperatures ranging between 24 and 29 °C (Henderson & Lucas, 1971). Larvae exposed to continual temperatures of 24–25 °C did not advance past the early brachiolaria stage. It would seem that the development of larvae is completed only within the temperature range of 25–32 °C (Lucas, 1973) and that maximum survival and development is achieved between 28 and 32 °C.

Salinity changes have been noted to affect the development of larval *A. planci*. Bipinnaria larvae were found to tolerate a wide salinity range (21–33‰) while later stages were less tolerant (Henderson & Lucas, 1971). Lucas (1973) reported that larvae completed their development in salinities as low as 26‰. He found, however, that survival of larvae was enhanced threefold in a salinity of 30‰ (Lucas, 1973, 1975).

Observations from laboratory studies suggest that while in the plankton, larvae exhibit negative geotaxis and are photopositive actively swimming towards the water surface, although it is possible that this movement may be disrupted by wave motion and water currents (Yamaguchi, 1973b). Very little is known about the dispersal of larvae in the field (Lucas, 1975) or the effects of water currents on larval dispersal and recruitment. Plankton

trawls were undertaken by Pearson & Endean (1969) in a bid to study larval dispersal but they were largely unsuccessful.

Towards the end of the brachiolaria stage when the larvae are about 1–1.2 mm in size they begin to drift downward and explore substrata to find a suitable surface on which to settle. It has been suggested that they settle mainly on dead corals and under boulders (Ormond *et al.*, 1973). Yamaguchi (1973a) observed in the laboratory that some larvae settled on dead coral covered with coralline (*Porolithon*) and other epiphytic algae. This was also noted by Henderson & Lucas (1971) although they found that the larvae did not settle on other substrata. They suggested that larvae may not settle if a suitable substratum is not found. Experiments by Lucas (1975) provided evidence to indicate that larvae did not require a particular surface but only one that possessed a biological film. Apart from not knowing what type of surface the larvae settle on in the field it is not known in which areas of the reef they settle. If they remain in the upper layers of the water column, it might be expected that they would settle in shallow areas on reefs (Ormond & Campbell, 1974). However, towards the end of the brachiolaria stage when a primordium is beginning to develop the larvae become negatively buoyant and tend to sink (Olson, 1985). This behaviour may result in larvae settling in areas of deeper water. This aspect will be discussed in more detail in a later section (see pp. 413–414).

GROWTH AND LONGEVITY

Studies of the growth of *A. planci* essentially have addressed the following four questions each of which will be discussed in turn in this section.

- (1) Does *A. planci* grow at the same rate throughout its life?
- (2) Does it grow continually throughout its life; *i.e.* is growth determinate or indeterminate?
- (3) Is it possible to determine the age of a starfish from its size?
- (4) How long does *A. planci* live?

One of the first studies of the growth rate of *A. planci* was undertaken by Pearson & Endean (1969) who obtained growth data from individual starfish kept in the field as well as the laboratory. From these studies they found that adults grew at a rate of between 9–14 mm a month while over the same time juveniles increased their diameter by 11 mm. They thought that growth after metamorphosis was rapid as they had found individuals up to 33.8 mm in size only two months after the spawning period. As a result they estimated that starfish could attain a size of 140 mm in almost 12 months assuming growth occurred at a linear rate of approximately 10 mm a month.

Studies have since demonstrated that starfish do not grow at a linear rate and that the initial growth of juveniles prior to transformation is slow. The newly metamorphosed juvenile starfish is between 0.3 and 0.5 mm in size (Henderson & Lucas, 1971; Yamaguchi, 1973b). Over the next four to five months the starfish, which feeds on algae grows to 8–10 mm in diameter (Yamaguchi, 1972a,b). The growth rate at this stage is exponential and the starfish may develop new arms at the rate of one every 9–10 days (Yamaguchi, 1975b). After about six months the juvenile starfish possesses all the

external features of an adult, with about 16–18 arms. At this point it begins to feed on corals (Yamaguchi, 1973b, 1974; Lucas, 1975). Once this transformation has been completed, the growth rate increases and starfish may reach a size of 60–70 mm within 1 year and 200 mm after 1.5–2 years (Yamaguchi, 1974b; Lucas & Jones, 1976). This phase of Von Bertalanffy-type growth (Lucas, 1984) continues at least until the starfish reaches sexual maturity. Most starfish become sexually mature late in their second year of life (Lucas & Jones, 1976).

Until starfish attain sexual maturity their growth is sigmoidal and may best be described by a logistic growth curve (Yamaguchi, 1975a). Studies by Yamaguchi (1974b) and Lucas (1984) demonstrated that the growth rate of starfish declines greatly once sexual maturity is attained. In other words, the growth of starfish tapers off approximately 20 months after metamorphosis. From his laboratory studies Lucas (1984) recognized a phase of non-growth in starfish at three years of age (about 350 mm). During this “senile” period the size of some individuals was found to decrease and gametogenesis also began to decline. Lucas (1984) indicated that this phase may last for several years after which time the starfish may die.

Laboratory studies by Yamaguchi (1973b, 1974b, 1975b), Lucas & Jones (1976), and Lucas (1984) indicate not only that the growth rate of *A. planci* is variable throughout its lifetime but also that its growth is determinate. Whether the growth of *A. planci* in the field is determinate has not been resolved. The studies mentioned previously have been criticized on the grounds that the results may be an artifact of laboratory conditions and that they may represent the effects of such factors as disease and infection (Kenchington, 1977). This was also suggested by Lucas (1984) who stated that the senile phase he observed in the laboratory may have been a consequence of a number of factors including; the size and volume of the aquaria, the absence of predation and the lack of environmental variability. He considered, however, that there was circumstantial evidence of senility occurring amongst starfish in the field. He referred to the studies of Branham *et al.* (1971) and Kenchington (1977) where they had measured the growth of isolated starfish populations over a year. The individuals in these populations grew very little during these studies and this was interpreted by Lucas (1984) as evidence of senility. Kenchington (1977), on the other hand, regarded that this lack of growth in both studies was due to local conditions which reduced the availability of food.

The debate surrounding the mode of growth of *A. planci* has continued because there are few data on the growth of individuals in the field. Kenchington (1977) stated that the growth of this starfish is indeterminate since individuals up to 700 mm have been found on reefs. This is not an isolated occurrence as there have been several reports of starfish greater than 500 mm in size on reefs (Chesher, 1969b; Laxton, 1974; Stanley, 1983; Moran, Bradbury & Reichelt, 1985). These findings would appear to conflict with those of Yamaguchi (1974b, 1975a) and Lucas (1984) who proposed that starfish ceased growing at a diameter of approximately 350–400 mm. Kenchington (1977) attempted to obtain information on growth from the field by analysing size frequency data which had been collected at different times from a number of reefs in the Great Barrier

Reef. By analysis of modes within size frequency distributions he identified a number of size classes within each sample group which were thought to be related to the age of starfish. A total of six year classes were determined for the entire number of samples ($n=7143$). Kenchington (1977) derived a growth curve from this information which gave values similar to those obtained in the field by Pearson & Endean (1969), although they did not reflect the early rapid growth phase (coral-feeding juvenile phase) described by Yamaguchi (1974b) and Lucas (1984).

The model presented by Kenchington (1977) demonstrated that *A. planci* grew initially at an exponential rate followed by an arithmetic increase in size. The growth curve derived from the size frequency data suggested that the growth of *A. planci* was indeterminate and that it did not stop after about three years of age as was proposed by Yamaguchi (1974b) and Lucas (1984). Kenchington (1977) argued that large starfish (>350 mm) found in the field may have undergone longer periods of exponential, or faster, growth. He concluded that if this were the case then large sexually immature animals should be found in populations on reefs. As this type of starfish has not been found in the field Kenchington (1977) proposed that the growth of *A. planci* was indeterminate. Lucas (1984), on the other hand, claimed that the occurrence of these large animals in the field would not be evidence of this type of growth but that they may have arisen due to genotypic and environmental variations, although he did not elaborate on these suspected causal factors. This debate will remain unresolved until intensive growth studies of individual starfish are carried out in the field over long periods.

The results of Kenchington's study have received further criticism. Ebert (1983) has stated that the data analysed by Kenchington (1977) were unsuitable as there had been little continuous sampling of the same sites through time. He pointed out as a consequence that it was not possible to define whether or not successful recruitment had occurred during the same year over the entire Great Barrier Reef.

While undertaking this study Kenchington (1977) made three assumptions; first, that the spawning period of *A. planci* was restricted to late December or January, secondly, that the growth of starfish was the same over all areas of the Great Barrier Reef and finally, that modes in a size frequency distribution corresponded to age classes that were separated by one year. This study has been criticized mainly on the grounds that there is little relationship between the size of a starfish and its age (Lucas, 1984). Other studies have been conducted which have ascertained the age of starfish on reefs from an analysis of the size frequency distribution of the population (Ormond & Campbell, 1971, 1974; Nishihira & Yamazato, 1972; Endean & Stablum, 1973b; Laxton, 1974) and they too have been criticized for the same reasons.

In the laboratory, Lucas (1984) demonstrated that the growth and size of starfish are governed by diet. He showed that the diameter of starfish fed on coral may be twenty times that of starfish fed on coralline algae for the same period of time. On the basis of this information he suggested that it was erroneous to assume that there was a correlation between the size of an individual and its age. It follows that the growth of starfish in the field will depend on the types of food available (Ormond & Campbell, 1971). Should

larvae recruit to an area which has a high coverage of encrusting algae and little coral, then their growth and size may be severely restricted. If they are unable to find coral, juvenile starfish may continue to feed on algae and their size may be much less than those of larvae that fortuitously settle in an area of high coral cover and that were able to change their diet quickly once they had attained adult morphology. Recently, studies have been conducted in Fiji where the growth of a large number of juvenile starfish was followed for over a year (L. Zann, *pers. comm.*). Initially they were similar in size but as the study progressed the size range of the starfish increased considerably. This gap was found to widen as some starfish began to feed on corals while others continued to feed on algae.

Observations in the field indicate that the growth and thus size of starfish may also be altered by several factors other than diet. Branham *et al.* (1971) reported that the diameter of starfish increased and decreased both before and after spawning. They also suggested that the mean size of individuals may be determined by population density. In Hawaii they found that the mean size of aggregated starfish was smaller (240 mm) than individuals that were sparsely aggregated (350 mm). The size of starfish may also be affected by handling. Yamaguchi (1974b) found that handling of *A. planci* may cause them to reduce their size by up to 20%. These findings highlight the need for care when interpreting the results of size frequency distributions (Feder & Christensen, 1966). It would seem that the usefulness of such a practice may be confined to making general statements about population structure (*e.g.* defining the occurrence of juvenile and adult sub-populations) rather than attempting to describe more detailed characteristics such as the age of various subgroups within a population.

Ebert (1983) considered that Kenchington's model indicated that *A. planci* was a relatively short-lived species since the populations declined to low levels several years after they appeared. While this model does indicate that the majority of starfish disappear from reefs (die?) it does not preclude the possibility that a small number of starfish may remain and live for many years. This raises the question as to what happens to the large numbers of starfish which seemingly vanish from reefs at the end of an outbreak. Do they move off into deeper water or to another reef or do they die? Studies by Glynn (1984b) have indicated that it may take at least 4 days for starfish to decompose in the field. Why then are newly-dead or decomposing starfish not sometimes observed on reefs, given the densities of individuals which may be present in outbreaks? The life expectancy of starfish in the field is unknown. Cameron & Endean (1982) hypothesized that *A. planci* must be a long lived species because it has specialized defensive structures (long venomous spines), few parasites and has certain specialized feeding adaptations (see p. 400). Chesher (1969b) suggested that *A. planci* may live for up to eight years but he gave no evidence to support this statement. In the light of studies by Lucas (1984) this figure may be realistic as he managed to keep some starfish in aquaria for almost this length of time despite the fact that others had died earlier from disease. Ebert (1973) applied a growth model to data from Hawaii (Branham *et al.*, 1971) and predicted that it would take almost 30 years for starfish to reach full size. In the light of current knowledge of the biology of *A. planci* this model would seem to be unrealistic. Accurate information on the longevity

of *A. planci* in the field may not be forthcoming until a true field study of the population dynamics of this starfish is undertaken.

FEEDING BIOLOGY

Experiments conducted in the laboratory by Lucas (1982) using diets of single species of unicellular algae have shown that there is an inverse relationship between the filtration rate of bipinnaria and brachiolaria larvae and food concentration. The maximum rates of filtration for these larval stages were recorded to be from $1.3\text{--}6.6\ \mu\text{l}$ per min. While this relationship is common to a number of echinoderms it was noted to be complex for certain of the larval stages of *A. planci*. Although the filtration rate declined as food concentration increased it was generally insufficient to cause a reduction in the rate at which food was ingested. Thus, there was a positive relationship between ingestion rate and food concentration. The highest rate of development and survival was achieved with food concentrations from $5\text{--}10 \times 10^3$ cells per ml (Lucas, 1982). During these studies seven species of algae were tested for their effects on larval development and survival. Of these, *Dunaliella primolecta* and *Phaeodactylum tricornutum* supported the most rapid larval development and highest survival. After comparing the results of these experiments with data (phytoplankton abundance and chlorophyll *a* concentrations) available from the Great Barrier Reef, Lucas (1982) concluded that the levels of phytoplankton normally found in the field were insufficient for the development of larvae of *Acanthaster planci*. Consequently, he postulated that "food is a major environmental influence on survival and development of *A. planci* larvae in these waters" (Lucas, 1982: p. 173).

This statement addresses the much debated issue of the relationship between larval abundance and phytoplankton concentration which Thorson (1950) considered an important problem in larval ecology. Despite being recognized as an important issue for many years, very little is known about whether larval starvation occurs in the field. It is generally thought that the two major causes of mortality of invertebrate larvae are predation and starvation (Vance, 1974). Starvation may affect the survival of larvae directly, by causing the death of the organism. It may also affect survival indirectly, by lengthening the larval phase (Lucas, 1982), thereby reducing the 'vitality' of larvae and increasing the potential for predation.

Lucas (1982) used chlorophyll *a* as a measure of phytoplankton biomass and compared his results (where larvae were fed on a single algal species) with concentrations in the field. While phytoplankton productivity in coral reef areas is generally considered to be low (Kinsey, 1983), it is not clear whether these conditions cause mass larval starvation. Rather, their effects on larval survival may be compensated for by the presence of a diverse range of phytoplankton species. Several studies have shown that a mixed diet of phytoplankton is beneficial to the survival of invertebrate larvae (Bayne, 1965; Gaudy, 1974). As yet, nothing is known about the likely benefits such a diet would have on the survival of larvae of *A. planci* in the field.

Bacteria and dissolved organic matter are two other possible sources of nutrition for larvae. Very little is known about their abundance in coral reef

waters or their nutritional importance to the larvae of *A. planci*. Lucas (1982) considered that bacteria may not be an important nutritional source as the larvae of *A. planci* may not be able to feed on them efficiently. He admitted, however, that there were no data on bacterial numbers in Great Barrier Reef waters. Dissolved organic matter has been shown to be used as a source of nutrition by echinoderm embryos (Strathmann, 1975). While Lucas (1982) agreed that organic molecules may be absorbed by echinoderm larvae, he stated that it was unlikely to be a major source of nutrition for the larvae of *A. planci*. Recent studies by Manahan, Davis & Stephens (1983) indicate, however, that 79% of the energy requirements of larvae of the echinoid *Strongylocentrotus purpuratus* could be supplied by amino acids which exist in a number of forms in sea water. Thus the rôle of dissolved organic matter in the nutrition of larvae of *Acanthaster planci* may prove to be more important than first thought.

Clearly, a great deal more research needs to be undertaken in this area. It is particularly important to determine the concentrations of phytoplankton, bacteria, and dissolved organic matter that are normally found in coral reef waters. In addition, experiments concerned with the effects of multiple species diets and alternative food sources such as bacteria and dissolved organic matter on the larval survival of *A. planci* need to be conducted. A more direct way of approaching the question of whether the larvae of *A. planci* normally starve in the field is to attempt to observe their development *in situ*. Olson (1985) has demonstrated that this type of approach is feasible. Using specially developed culturing systems he reared larvae of *A. planci* *in situ*, under nutrient conditions (at 5 and 15 m depths) which were thought to approximate natural food levels. Although survival was low, Olson succeeded in rearing larvae to the mid-brachiolaria stage. Larvae need to be reared to the late brachiolaria stage before conclusions can be drawn as to whether starvation is an important factor in their mortality. Olson (1985) pointed out that if starvation is important then it probably occurs during this later stage.

In reviewing the diet of *A. planci* Jangoux (1982a) considered that it was essentially a carnivore on corals (corallivore) and that it rarely fed on other animals. This statement, while correct, does not apply to the first six months of this starfish's life when it feeds on coralline and epiphytic algae (Yamaguchi, 1973b, 1974b, 1975b; Lucas, 1975). Even when it changes its diet, corals are not the only food that this starfish is capable of eating. There are numerous references in the literature to *A. planci* feeding on other types of food (Table IV). These range from anemones to soft corals and encrusting organisms. Most of the information given in Table IV has come from observations in the field. In captivity *A. planci* may be fed on fish, squid, and scallop meat as well as beef and echinoids (Branham, 1973; Yamaguchi, 1975b; Lucas, 1984). Cannibalism has also been observed under these conditions (Barnes, 1966; pers. obs.). It is likely that these foods are only eaten in captivity and would not be common food sources in the field. Sloan (1980) has discussed the effects that captivity may have on asteroid feeding.

From field observations it would appear that adult *A. planci* commonly feeds on corals and that it only feeds on other sources of food when there is very little coral available (Chesher, 1969b). Sloan (1980) has suggested that

TABLE IV

*Alternative foods of A. planci: *field observation*

Food	Reference
Other <i>A. planci</i> (cannibalism)	Barnes, 1966; Branham, 1973
Algae	
Coralline*	Barham <i>et al.</i> , 1973
Other*	Dana & Wolfson, 1970; Vine, 1972
Clams*	Pearson & Endean, 1969
Echinoids	Yamaguchi, 1975b
Encrusting organisms*	Branham, 1973
Fish, squid, scallop meat	Branham, 1973; Cannon, 1975; Lucas, 1984
Gastropods*	Clark, 1950
Gorgonians*	Dana & Wolfson, 1970; Barham <i>et al.</i> , 1973
Hydrozoan corals*	Chesher, 1969b; Barnes <i>et al.</i> , 1970
Sea anemones*	Verwey, 1930
Soft corals*	Pearson & Endean, 1969; Chesher, 1969a
	Laxton, 1974

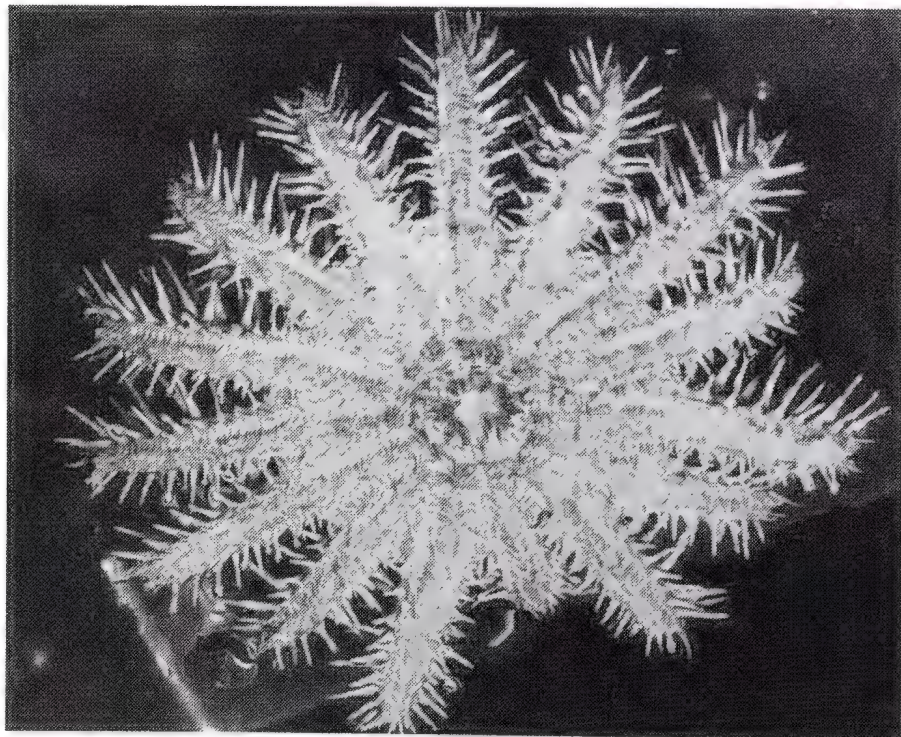


Fig. 4.—The ventral surface of a starfish (12 cm diameter) showing the mouth, and inside, part of the stomach (centre) (photograph taken by L. Brady).

A. planci is a specialist coral-feeder. Consideration of its feeding biology confirms this, as *A. planci* is an extraoral feeder (Jangoux, 1982b). When feeding it everts its stomach through its mouth and spreads this membraneous structure over an area of the coral surface equal to that of the oral disc (Goreau, 1964) (Fig. 4). The tube feet are used to position the stomach around the irregularities of the coral (Brauer, Jordan & Barnes, 1970). Once this has been accomplished the stomach secretes an enzyme which digests the coral tissue and the products are then absorbed (Goreau, 1964; Endean, 1973a). The feeding process may take from 4–6 h (Brauer *et al.*, 1970). The enzyme which is secreted is thought to have a proteolytic action (*i.e.* it hydrolyses proteins) as collagenase has been isolated from the stomach of *A. planci* (Yomo & Egawa, 1978). An additional enzyme (N-acetyl-B-D-glucosaminidase) has also been found in the pyloric caecum by Yomo & Tokumoto (1981). Proteolytic action in the stomach was greatest at pH 8.4 (Shou-Hwa, 1973); this may be an adaptation for extracellular uptake of food in sea water. Optimal proteolytic activity for the pyloric caecum was at pH 7.6.

In a recent review Jangoux (1982a) commented that the digestive system of *A. planci* was similar to that of starfish in the family Solasteridae although its stomach was much larger. The anatomy of the stomach as well as the pyloric and rectal caeca have been described by Hayashi (1939). *A. planci* is considered to be a specialist coral-predator (Cameron & Endean, 1982) partly because it has the unique ability to hydrolyse cetyl palmitate which is a major wax energy reserve in corals (Bensen, Patton & Field, 1975). A common feature of asteroids is that they can live for long periods (sometimes years) without feeding (Sloan, 1980). Observations of adults in captivity indicate that *A. planci* also has this ability and it may survive for up to six months without food (J. S. Lucas, pers. comm.; pers. obs.). Pearson & Endean (1969) starved three caged adults in the field for four months; at the end of that time they were alive and apparently healthy.

FEEDING BEHAVIOUR

There is much conflicting evidence concerning whether *A. planci* feeds nocturnally or diurnally. Several studies have indicated that the feeding behaviour of this starfish is related to population density. Chesher (1969b) stated that it was a nocturnal feeder when in low population densities. This was also confirmed by Pearson & Endean (1969) and Endean (1974) although they suggested that up to 90% of individuals in aggregations fed during the day on the Great Barrier Reef. This type of feeding behaviour was also noted in Hawaii (Branham *et al.*, 1971) and Micronesia (Cheney, 1974). These results conflict with those found elsewhere. In the Red Sea *A. planci* was primarily a nocturnal feeder even when in dense aggregations (Roads & Ormond, 1971). Similarly, Ormond & Campbell (1974) found that only 12% of starfish actively fed diurnally, irrespective of whether or not they were in aggregations. In contrast, Dana & Wolfson (1970) observed, in the Gulf of California, that starfish (*A. ellisii*?) fed during the day even though they were not aggregated. This was also recorded in Panama (*A. planci*) by Glynn (1972). In Western Australia, 30–50% of starfish were reported to feed during the day whether aggregated or not (Wilson & Marsh, 1974, 1975). From these findings it would seem that the feeding behaviour of *A. planci* is varied and shows little relationship to population density.

(Kenchington, 1975a; Kenchington & Morton, 1976). Experiments conducted in the laboratory have demonstrated that feeding behaviour may be dependent on the time of day and the physiological state of the animal. Brauer *et al.* (1970) found that a high proportion of starfish in aquaria fed during the night. During the following day the starfish showed a marked decline in their desire to feed when they were presented with coral extracts. In the field this behaviour is likely to be far more complex and variable as it may be affected by a number of factors including: location (*i.e.* type and density of coral) (Potts, 1981); environmental conditions such as temperature (Yamaguchi, 1973c, 1974a), exposure (Endean, 1973b); age of starfish (Goreau, Lang, Graham & Goreau, 1972; Laxton, 1974); time of year (*i.e.* during spawning season) (Beach, Hanscomb & Ormond, 1975); light levels (Rosenberg, 1972).

On encountering a live coral or extracts of coral *A. planci* has been observed to rear its arms and retract its tube feet (Barnes, Brauer & Jordan, 1970). This aversive response was shown to be due to the nematocysts released by the coral and also the chemicals derived from coral tissue (Moore & Huxley, 1976). The intensity of this response was found to depend on the nutritional state of the starfish (Barnes *et al.*, 1970). As it was initiated before contact with the coral this withdrawal response was thought to aid in protecting the tube feet of individuals. Starfish may overcome the effects of nematocysts in corals when attempting to feed by moving on their arms and spines (Barnes *et al.*, 1970). It would appear that these effects are not as pronounced during feeding as the stomach is less sensitive than the tube feet (Barnes *et al.*, 1970).

A number of studies have attempted to determine the factors responsible for inducing feeding in *A. planci*. Observations in the field by Ormond *et al.* (1973) indicated that *A. planci* preferentially attacked damaged corals or those already being eaten. Using Y-shaped aquaria they demonstrated that a chemical attractant was released when starfish fed which stimulated others to move towards the corals being eaten. Beach *et al.* (1975) found that movement could be induced by presenting the starfish with extracts of live coral. Earlier, Brauer *et al.* (1970) showed that feeding (stomach eversion) in *A. planci* also could be induced using these extracts. In a series of biochemical experiments conducted in the laboratory Collins (1974) was able to produce two sorts of responses from starfish using extracts of coral tissue. He was able to invoke a settlement (*i.e.* mounting and positioning of starfish on coral colony) and stomach eversion response and an arm retraction or avoidance response. High and low molecular weight fractions, which were separated and isolated from live coral tissue, were found to cause the settlement and stomach eversion of starfish. Collins (1975a) discovered that the low molecular weight fraction comprised amino acids and small peptides. The other fraction was macromolecular and was thought to be a glycoprotein. The entire coral extract was found to cause the withdrawal of arms and sometimes the retraction of tube feet. Collins (1975a) identified the substance which was primarily responsible for this avoidance response. It was chemically similar to the amino acid proline. During further experiments Collins (1975b) found that the intensity of the avoidance response could be altered by using extracts from different types of corals. Later experiments by Hanscomb, Bennett & Harper (1976) showed that

high molecular weight mucoproteins from coral mucus produced a feeding response in *A. planci*.

Sloan & Campbell (1982) have thoroughly discussed the evidence for the chemical perception of corals by *A. planci*. They pointed out that under certain conditions asteroids may be "pursuers" rather than "searchers" of prey. That is, they have the ability to perceive their prey, at short distances, and hunt them down. *A. planci* would also appear to have this ability although it may be affected by local environmental conditions (Sloan & Campbell, 1982).

There are some data on the feeding rate of *A. planci* and this has been derived from studies in the field and in the laboratory. Pearson & Endean (1969) determined the feeding rate of individual adult starfish of average size which were kept in cages on a reef. They found that these starfish consumed between 116 and 187 cm² of coral tissue per day. This represents a feeding rate of about 5.8 m² of coral tissue per year (Potts, 1981). Feeding rates of between 5 and 6 m² per year have been reported in the field from studies conducted in Panama (Dana & Wolfson, 1970; Glynn, 1973). Cheshier (1969b) reported that starfish in Guam fed on 378 cm² of coral tissue per day or approximately 12 m² per year. This rate is twice that recorded in other parts of the world and must be treated with some scepticism as Cheshier (1969b) gave very little information as to how this figure was derived. In the laboratory Yamaguchi (1974b) found that a juvenile of average size may kill around 200 g of *Pocillopora damicornis* in a day (based on the amount of dry coral skeleton mass killed). This may increase to about 300 g of coral per day or 100 kg per year for adult specimens. In general the feeding rate of *Acanthaster planci* will depend upon the same factors affecting its feeding behaviour.

FEEDING PREFERENCES

Experiments conducted in the laboratory have shown that *A. planci* prefers to feed upon certain types of corals (Brauer *et al.*, 1970). Coral extracts from *Acropora* and *Pocillopora* were found to produce stomach eversion whereas those from *Porites* mainly caused withdrawal responses. Collins (1975b) demonstrated that the type of coral consumed by a starfish may depend on its previous dietary experience. In the laboratory he demonstrated that *Acanthaster planci* learnt to differentiate between corals it had eaten previously and those that it had not encountered before. In general, *Acropora* spp. were found to be acceptable as food irrespective of the previous diet of the starfish. Ormond, Hanscomb & Beach (1976) also reported this type of learnt behaviour. They found that *Acanthaster planci* would feed more readily on corals that it had experienced before and that over a given time it reduced its feeding responses to coral extracts. Exploring this learnt behaviour further Collins (1975b) showed that starfish could be conditioned to eat species of coral (*e.g.* *Fungia*) which they may initially refuse. This was also reported by Huxley (1976) and Ormond *et al.* (1976) who stated that this type of learnt behaviour may persist for some time. Huxley (1976) commented that starfish learnt in time to determine the difference between coral extracts and live coral. He proposed that they may be able to detect the lack of some important dietary requirements as the

coral extracts aged over the period of the experiments. Therefore, the acceptability of a particular type of coral may well depend on its nutritional value (Ormond *et al.*, 1976).

From the results of these laboratory studies, *Acanthaster planci* would appear to favour feeding on commonly occurring corals such as *Acropora*. This is probably why *Acanthaster planci* has been observed to prefer this coral in the Great Barrier Reef (Pearson & Endean, 1969), where it tends to be the most common genus (J. E. N. Veron, pers. comm.), and not in some other parts of the Indo-Pacific region (*e.g.* Red Sea) where it may be less common (Ormond *et al.*, 1973). Potts (1981), however, has pointed out that while this starfish may feed predominantly on more abundant corals they may not be the most preferred species. Apart from learnt behaviour, a variety of factors are likely to influence the feeding preferences of starfish in the field. Those factors (some already have been discussed in previous sections) which may be responsible for determining the types of corals which are consumed by *A. planci* are as follows.

- (1) Nutritional state of starfish (Brauer, Jordan & Barnes, 1970).
- (2) Release of substances (*e.g.* nematocysts, mesenteric filaments) by corals (Barnes, Brauer & Jordan, 1970; Goreau *et al.*, 1972).
- (3) Release of chemical attractants by corals (Ormond *et al.*, 1973).
- (4) Learnt behaviour of starfish (Collins, 1975b; Huxley, 1976; Ormond *et al.*, 1976).
- (5) Abundance and distribution of corals (Ormond *et al.*, 1973).
- (6) Accessibility of corals (Barnes *et al.*, 1970).
- (7) Environmental conditions (Endean, 1973b; Ormond *et al.*, 1973).
- (8) Morphology of corals (Chesher, 1969a; Ormond & Campbell, 1974; Menge, 1982).
- (9) Commensal organisms in corals (Glynn, 1976, 1977, 1980, 1982a).
- (10) Nutritional value of corals (Ormond *et al.*, 1976).

Most of the information on feeding preferences in the field has come from qualitative studies as noted by Potts (1981). Of the numerous reports available on this topic there are really only three studies where *A. planci* has been demonstrated to show a preference for a particular type of coral or corals. In two of these studies starfish were reported to feed on corals which were considered to be less abundant. Branham *et al.* (1971) noted in Hawaii that 80–90% of *A. planci* fed on *Montipora verrucosa* despite the fact that this coral made up only 5% of the total coral cover. Similarly, Glynn (1974, 1976) showed that almost 50% of the diet of starfish in Panama was comprised of species that were comparatively rare (*i.e.* comprising only 7.2% of total coral cover). Laboratory and field experiments showed that *Acanthaster planci* tended to avoid the most common coral (*i.e.* *Pocillopora*) because it contained symbionts (the shrimp *Alpheus lottina* and the crab *Trapezia* spp.) which used chemical cues to detect and subsequently attack it when feeding. These animals were 31% effective in preventing *Acanthaster planci* from mounting and feeding on this coral (Glynn, 1976, 1980). In contrast to these results, Ormond *et al.* (1976) stated that in the Red Sea *A. planci* preferred the most abundant corals (*e.g.* *Pocillopora* and *Acropora*). This preference was, however, not well defined as the informa-

tion they presented was somewhat conflicting. For a more detailed account of the results of these studies refer to Potts (1981).

While all three of the studies described above provide the best information to date on feeding preferences in the field they were inadequate for either of two reasons. First, they relied fully or partly on qualitative assessments of the amount of coral eaten and the abundance of each coral genus (e.g. Branham *et al.*, 1971). Secondly, they attempted to demonstrate feeding preference by comparing the proportion of a particular type of coral eaten with its proportion at a community or reef level. As the distribution of corals may be patchy over different scales of the system (Reichelt & Bradbury, 1984; Bradbury, Hammond *et al.*, 1985) this comparison may have little meaning. Indeed, feeding preference may also vary in conjunction with these changes in coral distribution. Perhaps a better method of assessment would involve a comparison at the coral colony level rather than at the community level.

Apart from these studies there has been reference to the feeding preference of *Acanthaster planci* in a number of areas in the Indo-Pacific. Goreau (1964) noted that this starfish appeared to favour no one particular coral species in the Red Sea. In the Gulf of California *A. planci* was considered an "obligate feeder" as feeding preference depended on the distribution of corals (Barham, Gowdy & Wolfson, 1973). Coral genera such as *Pocillopora* (Glynn, 1976), *Porites*, *Galaxea* (Barnes *et al.*, 1970), and *Diploastrea* (Endean & Stablum, 1973a,b) have been reported to be not eaten by starfish in the field. This is not consistent, however, as in other parts of the world some of these corals (e.g. *Porites*, *Pocillopora*) have been observed to be eaten by *Acanthaster planci* (Dana & Wolfson, 1970; Goreau *et al.*, 1972; Nishihira & Yamazato, 1972, 1973; Nishihira *et al.*, 1974; Aziz & Sukarno, 1977). Of all corals *Acropora* (particularly tabular and branching forms) appears to be one of the most preferred (Chesher, 1969a,b; Pearson & Endean, 1969; Roads, 1969; Garlovsky & Bergquist, 1970; Nishihira & Yamazato, 1972; Aziz & Sukarno, 1977). There are several other studies which have reported additional information concerning the feeding preferences of *Acanthaster planci* (Campbell & Ormond, 1970; Weber & Woodhead, 1970; Ormond & Campbell, 1974). It is difficult to determine from the information given above whether *A. planci* shows definite feeding preferences as most of the evidence is qualitative. A series of intensive quantitative field studies involving densities of starfish and different types of coral communities is needed to enable a more accurate understanding of feeding preferences in *A. planci*.

MOVEMENT

Some information is available on the rate of movement of adult starfish in the field (Table V). Pearson & Endean (1969) reported that adults were capable of moving at a rate of about 20 m per hour over sand. The maximum rates of movement in other parts of the Indo-Pacific (Gulf of California, Red Sea, and Indonesia) were found to be almost half this figure. Data on the movement of juvenile starfish have come from aquarium studies. Yamaguchi (1973b) found that juveniles of 1 mm in diameter (2 weeks old) moved at a rate of about 1.0 mm per min (0.06 m per h).

Larger juveniles (19–70 mm) were recorded to move at speeds of between 1.4–4.0 m per hour (Pearson & Endean, 1969) (Table V). In addition, it has been reported that certain arms may lead during periods of movement indicating that *A. planci* may have a posterior-anterior axis (Rosenberg, 1972).

While *A. planci* is capable of relatively fast movement over coral reef substrata it is not known how long this rate can be maintained. More long-term studies of starfish movement have indicated that they may move up to 580 m in a week (Roads & Ormond, 1971). In Guam, individuals travelled a distance of approximately 250 m over the same period of time (Chesher, 1969a).

Other studies have shown that the movement of starfish is non-random over the scale of metres. Uni-directional movement, of several hours duration, has been observed in transplanted starfish (Branham *et al.*, 1971) and using time-lapse photography on the Great Barrier Reef (P. W. Sammarco, pers. comm.). In American Samoa, Beulig, Beach & Martindale (1982) studied the movement of groups of starfish of three different types of densities. Over 24 hours each group moved consistently in a different direction.

It is likely that several factors determine the rate and direction of movement of starfish. Barham *et al.* (1973) has suggested that the rate of movement is dependent on the density of coral. They found that *A. planci* moved at 0.6 m per hour in areas with low coral cover and at 0.25 m per hour at sites where the corals were more dense. Ormond & Campbell (1974) also proposed that starfish movement may be affected by environmental factors, particularly wave action, exposure, and perhaps light. Apart from coral density and various environmental factors it is possible that other variables are important in influencing the movement of starfish. These include: age, condition and nutritional state of the starfish; time of day; and type of substratum.

It is suspected that starfish move in large populations from one reef to another once the supply of food is exhausted (Endean, 1969; Talbot & Talbot, 1971). There are two main reasons for proposing this and they are based on circumstantial evidence. First, it has been reported that starfish first appear in deep water and then move up the reef slope consuming corals as they go (Moran, Bradbury & Reichelt, 1985). Secondly, the starfish comprising these initial stages of the outbreaks are not usually juveniles but

TABLE V

*Rate of movement of juvenile and adult A. planci: *field observation*

Starfish	Rate (m·h ⁻¹)	Reference
Juvenile	0.06	Yamaguchi, 1973b
Juvenile	1.4–4.0	Pearson & Endean, 1969
Adult*	20.0	Pearson & Endean, 1969
Adult*	10.0	Barham <i>et al.</i> , 1973
Adult*	5.0–10.0	Goreau, 1964
Adult*	0.3–8.0	Aziz & Sukarno, 1977

tend to be 2–3 years old (Endean, 1973b). While these observations may provide evidence to support the notion that starfish move between reefs, the sudden appearance of large starfish in deep water may be explained equally well if they originated from larvae which settled in deep water at the base of a reef.

There is indirect evidence to suggest that starfish are capable of moving large distances between reefs. The information presented above indicates that they can move rapidly over various types of reef terrain. They are able to go for long periods of time without feeding. This information, however, was based on animals in captivity and not on ones that were highly active. Starfish have been observed to cross large expanses of sand between patch reefs (Pearson & Endean, 1969). They have also been dredged from deep water (64 m) between reefs (Great Barrier Reef Marine Park Authority, unpubl. data). Unfortunately there is no conclusive proof that starfish move in large numbers between reefs.

PHYSIOLOGY

Few studies have been reported on the physiology of *A. planci*. Those by Yamaguchi (1973c, 1974a) represent essentially the only attempts to investigate this particular facet of the biology of this animal. From these experiments it was demonstrated that *A. planci* is a "metabolic conformer" as its rate of oxygen consumption is determined by changes in environmental temperature and possibly other variables. Maintenance of a normal metabolism and behaviour occurred up to a temperature of 31 °C. Increases in temperature to 33 °C were observed to cause abnormal behaviour, the cessation of feeding, and disruption to the metabolic activity of individual starfish. Prolonged exposure (about 1 week) to this temperature regime caused the eventual death of starfish. This led Yamaguchi (1974a) to postulate that adult *A. planci* may avoid reef flat environments, where high temperatures may occur, as they may not be able to maintain a constant oxygen metabolism.

METABOLISM OF STEROIDS

Numerous studies have been carried out which have sought to isolate sterols and other steroid-related compounds from *A. planci*. Experiments of this sort have been conducted on a variety of echinoderms (Voogt, 1982). They are important from a theoretical perspective as echinoderms are thought to be closely related to vertebrates. Many of the metabolic processes identified in echinoderms parallel those found in vertebrates. Isolation of sterols and steroid-related substances from echinoderms may provide a better understanding of the metabolic processes of vertebrates and how they evolved.

In vertebrates, sterols are important structural components of cell membranes and are the antecedents of steroids and cholic acids (Voogt, 1982). A number of sterols were identified in *A. planci* by Gupta & Scheuer (1968). The chemical structure of one of those (acansterol) was isolated and described in detail by Sheikh, Djerassi & Tursch (1971). They argued that this sterol was a derivative of gorgosterol which occurs in coelenterates such as corals. The existence of this pathway was verified by Kanazawa,

Teshima, Ando & Tomita (1976) who succeeded in isolating an intermediate compound called gorgosterol.

The occurrence of gorgosterol indicated that the composition of sterols in *A. planci* may be a function of diet. Experiments by Sato, Ikekawa, Kanazawa & Ando (1980) identified the chemical structures of the various sterols present in *A. planci*. The most dominant group of sterols in this starfish were Δ^7 sterols. Kanazawa, Teshima, Tomita & Ando (1974) showed that this starfish contained sterols which were similar to those found in other coral reef organisms thus indicating that they may have been derived through the food chain. Experiments by Teshima, Kanazawa, Hyodo & Ando (1979) also demonstrated that the sterols in *A. planci* may be transferred to a known predator, *Charonia tritonis* (giant triton), as the sterol composition of both animals was found to be similar.

Another group of compounds called saponins have been isolated from *Acanthaster planci*. These substances are derived from steroids and are toxic to various marine animals (Voogt, 1982). Numerous studies by Croft, Fleming & Howden (1971), Sheikh, Tursch & Djerassi (1972a,b), Shimizu (1971, 1972), Sheikh & Djerassi (1973), Sheikh, Kaisin & Djerassi (1973), Howden, Lucas, McDuff & Salathe (1975), and Fleming, Salathe, Wyllie & Howden (1976) have resulted in the identification of at least four different saponins from adult *A. planci*. Similar compounds have been found in comparable amounts in the eggs, ovaries, and larvae of this starfish (Howden *et al.*, 1975; Lucas, Hart, Howden & Salathe, 1979). Further characterization of the chemical sub-units of the saponins isolated from *A. planci* have been conducted by Kitagawa, Kobayashi, Sugawara & Yosiooka (1975), Kitagawa & Kobayashi (1977, 1978), Kitagawa, Kobayashi & Sugawara (1978) and Komori *et al.* (1980, 1983a,b). The potential anti-predator rôle of saponins in larvae is discussed later (see p. 415).

ECOLOGY OF *A. PLANCI* POPULATIONS

INTRODUCTION

Many studies conducted in the field have involved surveys which have attempted to determine the distribution and abundance of starfish and/or corals on reefs. Numerous surveys have been undertaken on the Great Barrier Reef (see p. 431) and on reefs in Micronesia (Chesher, 1969a; Marsh & Tsuda, 1973) over the last 20 years. From the information given in the previous section it becomes apparent that very few attempts have been made to investigate more detailed aspects of the ecology of *A. planci* populations. This general lack of research has occurred at all stages of the life history of this animal. Studies of the larval ecology of *A. planci* have included preliminary, *in situ*, rearing experiments (Olson, 1985) and extensive plankton sampling programmes on the Great Barrier Reef (Pearson & Endean, 1969; Walsh *et al.*, 1976). Despite intensive efforts these latter studies were unsuccessful as no *A. planci* larvae were identified. Only one intensive field study of juveniles has so far been reported (see p. 396). Similarly, there has also been a lack of studies on adults in the field. Those

that have been conducted have concentrated on investigating the movement and behaviour of individuals or aggregations over relatively short time intervals, measuring the size of individual starfish, recording the density of starfish over well-defined but small areas and determining the feeding preferences of starfish. To date, little information is available about the population dynamics of *A. planci*. Field data on growth, longevity, mortality, and to a lesser extent, movement and feeding rate are inadequate. These data are essential in order to achieve a basic understanding of the dynamics of *A. planci* populations.

The general lack of field studies on all aspects of the life history of *A. planci* has arisen mainly because experimentation on larvae, juveniles or adults has proved logistically difficult. The larvae of *A. planci* are difficult to study since they are very small and may often be dispersed by ocean currents. While juveniles are much bigger than larvae they are none the less difficult to find in the field because they are extremely cryptic and capable of inhabiting very small crevices and holes in the reef substrata. In contrast to larvae and juveniles, adults may be easily found on reefs from time to time especially during outbreaks but it is difficult to study these types of starfish in the field as they are not amenable to tagging and hence individuals cannot be recognized or followed over long periods. Most field studies of adults were designed to obtain data about entire populations (e.g. size frequency data) and have not presented long term information on individual starfish. It is obvious that future research must be concentrated in these areas if a greater understanding of the *Acanthaster* phenomenon is to be achieved.

DISTRIBUTION AND ABUNDANCE

Copious data exist on the distribution and abundance of starfish following numerous surveys conducted throughout the Indo-Pacific region over the last 20 years. The data are not definitive assessments of the distribution and abundance but represent only broad estimates of starfish populations. There are several reasons for this.

- (1) Reefs may be such large and complex structures that they cannot be surveyed accurately using current techniques.
- (2) The starfish are often cryptic and their abundances are difficult to estimate; this may become even more arduous when outbreaks occur, as often their abundances are so high that they cannot be counted effectively.
- (3) Animals may be distributed unevenly over the reef surface and the results obtained for one area may not reflect those on the reef as a whole; thus extrapolating the results for small areas to indicate the likely abundance of starfish over entire reefs requires care.

Starfish abundance has little meaning if it is not compared with some type of standard measure. There have been several attempts at standardization when assessing starfish populations. For example, Pearson & Endean (1969) observed 405 starfish in 5 min of searching at the Frankland Islands. They also reported finding 1150 individuals in 20 min at Green Island. Different figures have been reported from other parts of the Indo-Pacific. Glynn

(1974) recorded a maximum density of 1 starfish per 50 m² on reefs in Panama while Branham *et al.* (1971) found 158 starfish in a circular area, 10 m in radius. In Okinawa, Nishihira & Yamazato (1974) reported finding an average of 241.5 starfish for every 10 min of searching while in the Fijian Islands Randall (1972) recorded 510 starfish in 100 min. There are many more references in the literature to this type of information (see Potts, 1981). Perhaps the best estimates of the maximum number of starfish which may occur during outbreaks come from the numbers of individuals killed during control programmes (see Table XIV, p. 450). Those conducted in Hawaii destroyed two groups, each of about 10 000 individuals, within a two-year period (Branham *et al.*, (1971). Approximately 44000 starfish were removed from a small area on Green Island over about 18 months while over a similar length of time almost 490 000 individuals were destroyed in American Samoa (Birkeland & Randall, 1979). The results obtained from control programmes indicate that outbreaks may consist of hundreds of thousands, perhaps even millions of starfish (Yamaguchi, in press). Similar levels of abundance were reported for the outbreak that occurred at Green Island during 1979–1981 (Endean, 1982). Taken as a whole, data from starfish surveys and control programmes serve to highlight the extreme variability that can occur in the abundance of starfish on reefs.

Not only is the abundance of starfish on reefs highly variable but so also is their distribution. Numerous surveys have demonstrated that starfish do not occur evenly over the surface of reefs but tend to form localized concentrations or aggregations (Fig. 5) (Ormond & Campbell, 1974; Endean & Stablum, 1975; Birkeland, 1979). These are thought to be the result of several factors whose effects may be cumulative over a given period (Sloan,

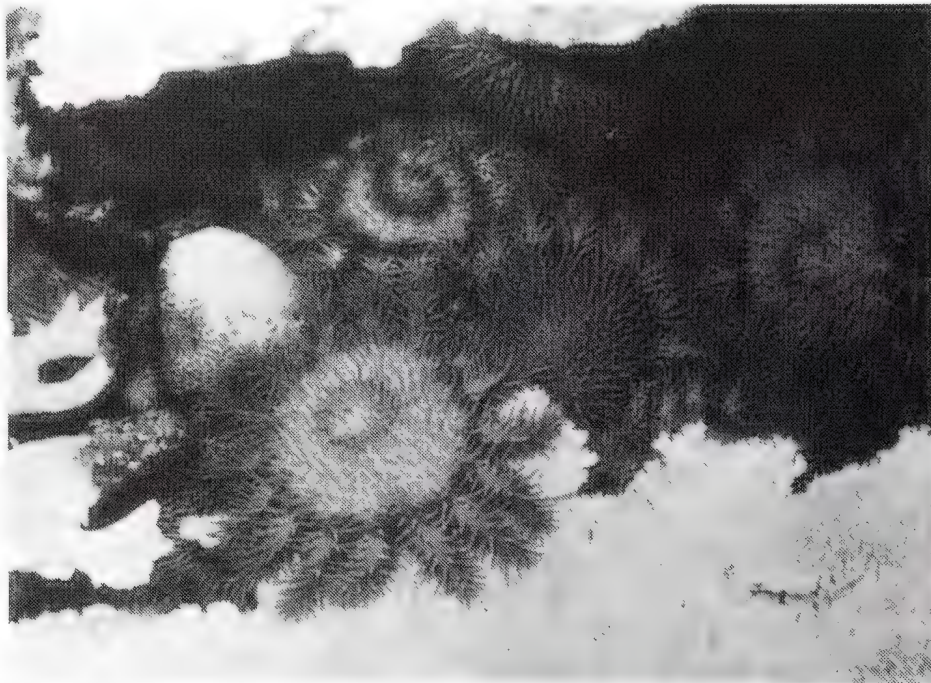


Fig. 5.—An aggregation of adult starfish.

1980). Factors which may be important in causing the formation of such aggregations are: presence of spawning attractants and coral extracts, age of starfish, distribution and abundance of coral, type of coral, stage of outbreak, and environmental preferences (*e.g.* depth, type of substratum, light and type of exposure) (Endean, 1974; Sloan, 1980). While the spatial distribution of starfish is uneven on reefs it also may vary temporally as the aggregations themselves may move. Endean (1969) suggested that this occurs once the food supply has been exhausted on a section of reef. Aggregations have been reported to move at a rate of approximately 100 m per month (Ormond *et al.*, 1973; Ormond & Campbell, 1974) and persist for up to 2 years. In Guam, Chesher (1969a) reported that aggregations travelled approximately 3 km in a month although feeding during this time was probably reduced as the movement occurred over dead or poorly developed reef.

The distribution and abundance of starfish on reefs varies over both temporal and spatial scales (Moran, Reichelt & Bradbury, 1985). While most surveys have managed to demonstrate that starfish abundances vary spatially few, if any, have described the pattern of change in the distribution and abundance of starfish over a complete outbreak cycle (*i.e.* before, during, and after an outbreak). This is because most surveys have not been carried out repeatedly over the same areas through time. The few attempted (*e.g.* Kenchington & Morton, 1976) were not conducted at short enough intervals of time nor were they undertaken over long enough periods. Recently Moran, Bradbury & Reichelt (1985) reported the results of surveys where changes in the abundance and distribution of starfish were followed before, during and after an outbreak over 2 years on John Brewer Reef. Prior to the outbreak, starfish were rare; only four individuals over 10 km of the reef perimeter were observed. Within 12 months the population had, however, increased dramatically with an average of up to 100 starfish being recorded for each two-min manta tow. After a further three months starfish numbers had declined again to relatively low levels (<7 per two-min tow). An interesting result emerged from these surveys. At the start of the outbreak starfish were concentrated on the fore-reef slopes but over a 9-month period they became more abundant in sheltered back-reef areas. This pattern of change in the distribution of starfish has been reported from other reefs in this region. For example, Laxton (1974) reported that this took at least two years to occur on Lodestone reef. In another study Kenchington (1976) found that the change in the distribution of starfish from front- to back-reef areas occurred within 12 months on several reefs. The tendency for adult starfish to seek sheltered back-reef areas may be because their powers of adhesion appear to decline with age (Ormond & Campbell, 1971; Goreau *et al.*, 1972). The rate at which this change occurs may depend on the size and structure of the reef, the distribution and abundance of live coral, the age and physiological state of the starfish, and environmental conditions (Moran, Bradbury & Reichelt, 1985).

While surveying the population repeatedly through time on John Brewer Reef, Moran, Bradbury & Reichelt (1985) measured the diameter (from arm tip to arm tip) of some 1200 starfish. Their mean size, 346.0 mm, indicated that the outbreak consisted primarily of adults. This is a feature common to

most outbreaks of starfish. Measurements in other areas have demonstrated that outbreaks generally consist of adults ranging in size from 250–350 mm (Chesher, 1969a; Pearson & Endean, 1969; Branham *et al.*, 1971; Ormond & Campbell, 1971; Owens, 1971; Cheney, 1974). Investigations of the size frequency distributions of these outbreaking populations have often shown them to be unimodal, comprising essentially one size class. Dana, Newman & Fager (1972) concluded that populations of starfish in Saipan, Kapingamarangi, and the Gulf of California were characteristically unimodal as were also populations in Fiji and Panama (Owens, 1971; Glynn, 1973). While some populations have been reported to be unimodal others have been considered to be polymodal, consisting of two or more size classes. Such populations have been reported on the Great Barrier Reef (Endean, 1973b), Japan (Suzuki, 1975; Moyer, 1978; Fukuda & Miyawaki, 1982; Matsusita & Misaki, 1983), and the Red Sea (Ormond & Campbell, 1971). Whether or not a population is represented by a polymodal or unimodal size frequency distribution may well depend on the time at which the measurements were undertaken. Moran, Bradbury & Reichelt (1985) found that initially the starfish population on John Brewer Reef was unimodal and dominated by one size class (at about 350 mm). Following additional measurements of the population on this reef after six months two distinct size classes were identified; one mode at approximately 300 mm and the other at 100 mm. They postulated that this latter mode represented recruitment possibly from the previous spawning period. Juveniles as small as 30 mm were recorded in this outbreaking population. This shift in the modal structure of outbreaks, caused by the influx of juveniles into adult populations has been mentioned by other authors (*e.g.* Endean, 1973b). Such events have been reported on rare occasions on several reefs in the Indo-Pacific (Pearson & Endean, 1969; Birkeland, 1982; L. Zann, pers. comm.).

At best, single, one-off surveys of reefs give only a snapshot view of outbreaking populations and do not indicate any temporal changes that may be occurring. Repeated intensive surveys of reefs are required to understand more about the dynamics of the behaviour of outbreaks, particularly whether they are declining or changing their position and whether additional recruitment to the population has occurred. This information is particularly relevant when attempting to undertake effective control programmes (see pp. 448–454).

RECRUITMENT

A feature common to many tropical marine species is that adults are conspicuous in the field while juveniles are rarely seen (Yamaguchi, 1973b). This is particularly noticeable in the case of *A. planci* where outbreaks of adults are commonly observed yet those of juveniles are not. As a consequence while there is some information on the ecology of adult *A. planci* there is practically no information on the processes that occur in the field between the time an egg is fertilized to its first appearance as an adult (about 250–350 mm in diameter). This is a grey area in the ecology of *A. planci* and is perhaps the main reason why the *Acanthaster* phenomenon is so poorly understood. One way of overcoming this situation is to obtain

information on the recruitment of this starfish. In a recent review Ebert (1983) defined recruitment as the "addition of new individuals to a population" (p. 169) and stated that this may be a result of immigration or reproduction. An investigation of recruitment is extremely important because it may lead to a greater appreciation of the reasons for fluctuations in the distribution and abundance of adult populations. The recruitment of many coral reef species is highly variable (Ebert, 1983) since it has been shown to be sporadic, varying in time and place (Frank, 1969; Sale, 1980). Thorson (1961) suggested that this type of recruitment was indicative of animals that were highly fecund and whose larvae were widely dispersed.

It has been postulated that large fluctuations in the abundance of *A. planci* are the result of differential survival of larvae (Birkeland, 1982) rather than any other stage. Yamaguchi (1937b) has pointed out that the survival of larvae and early juvenile stages may be variable but emphasized that there was hardly any information to verify this supposition. Lucas (1975) suggested the following factors which may be important in affecting the survival of these stages: degree of fertilization, abundance of food, temperature, salinity, extent of predation, dispersal and availability of suitable substrata for settlement. The last two are considered below (see earlier sections for a discussion of the other factors).

One of the most difficult things to determine about larvae is their likely dispersal before settlement and metamorphosis. Cheney (1974) has suggested that the increased recruitment of *A. planci* in Micronesia, specifically Guam, may well be a result of eddy systems which capture larvae and prevent them from being transported into deep oceanic water where they would most probably die. He found evidence which indicated that often outbreaks of *A. planci* were found on reefs where these eddy systems were prevalent. Such self-seeding of reefs may be important in Micronesia as many of the reefs are separated by large expanses of deep water. Rowe & Vail (1984b) have argued in a similar vein, suggesting that eddies and gyres may be responsible for the retention of *A. planci* larvae on some reefs in the Great Barrier Reef. They postulated that these current patterns may lead to recurrent outbreaks of starfish on the same reefs. More recently, Williams, Wolanski & Andrews (1984) have developed a model of the current patterns in the central section of the Great Barrier Reef. Using this model they showed that there was a tremendous potential for larvae to be dispersed over large distances in this region. During summer, the currents in shallow water (*i.e.* <40 m) were found to move in a net southerly direction at a rate of up to 300 mm per s. In deeper water the currents moved in the same direction but at about one third the speed. Given the relatively long larval life of *A. planci*, it is possible that a cloud of larvae released from mid-shelf reefs off Cairns may, after three weeks, be located adjacent to reefs near Townsville, a distance of some 300 km (see Fig. 7, p. 431). The model of Williams *et al.* (1984) lends support to that put forward by Kenchington (1977) which was based on analyses of the size frequency distributions of starfish from a number of different reefs. The model proposed by Kenchington suggested that recruitment of starfish in areas south of Cairns occurred in a series of three major waves (*i.e.* reefs off Innisfail-1964/66: reefs off Townsville-1967/69: reefs south of Townsville-1970/72) moving southwards (Fig. 7). The actual pattern of

outbreaks observed in this region broadly agrees with the models put forward by Williams *et al.* (1984) and Kenchington (1977) (see p. 434). When combined with the larval recruitment hypothesis (Pearson, 1975b) or the terrestrial run-off hypothesis (Birkeland, 1982) (see p. 462), these models provide an extremely plausible mechanism for the propagation of outbreaks on the Great Barrier Reef. Some questions are, however, still unresolved regarding this mechanism. First, it relies on the fact that a concentrated patch of larvae (larval cloud) is produced in areas where there are outbreaking populations. Despite intensive efforts to locate larvae near such populations none have ever been identified in plankton trawls (Pearson & Endean, 1969). Secondly, in view of the findings of Lucas (1982) (who suggested that natural food levels were insufficient for the survival of larvae), the larval cloud presumably would need to travel with, or pass through nutrient-rich patches or regions of food that would keep the larvae viable for the length of time they were in the water column. This is quite likely to be many days as the model by Kenchington (1977) indicated that the larval cloud may travel up to 100 km. Finally, each successive wave of larvae would need to be synchronized with the occurrence of these phytoplankton blooms. To date, there is no evidence to suggest that such conditions ever occur on the Great Barrier Reef (see p. 397).

Yamaguchi (in press) has proposed that larvae may be dispersed over great distances in accounting for the occurrence of outbreaks on the mainland of Japan and at Miyake Island (Fig. 6, p. 422). He postulated that outbreaks in Japan were a result of larvae that were transported by the warm Kuroshio Current from the Ryukyu Islands. Outbreaks at Miyake Island were thought to have originated when this current changed its course and left the main coast of Japan. As with the models proposed for the Great Barrier Reef, that postulated by Yamaguchi does not indicate whether the larvae are able to survive these long periods of travel. Larvae released as a cloud in the Ryukyu Islands would need to travel approximately 700–800 km to reach Miyake Island. More detailed oceanographic and planktonic studies are required in order to determine whether this is possible.

The survival of larvae depends not only on dispersion but also on whether there are suitable surfaces available upon which the larvae can settle. The extent to which this takes place can be gauged by estimating the numbers of small juveniles present on reefs. As mentioned previously, this is a difficult task as they are extremely cryptic and hard to locate. Yamaguchi (1973b) found few juveniles on the reefs at Guam despite searching intensively. This task is made even harder since it is not definitely known where larvae settle in the field. As the juvenile stages of *A. planci* feed on coralline algae it is often presumed that they settle on substrata where this food is available. Indeed, Yamaguchi (1973b) observed them to settle on these types of substrata in the laboratory, although Lucas (1975) considered that there was some evidence to indicate that all they required was a substratum that possessed a biological film. Because coral colonies killed by *A. planci* are quickly covered by epiphytic and coralline algae it has been suggested that this starfish provides an attractive substratum for the settlement of its own progeny (Chesher, 1969a; Ormond *et al.*, 1973). As yet no studies have been conducted to determine whether the larvae of *A. planci* prefer specific types

of coralline algae on which to settle. Indeed, little is known about the factors which are important in governing the settlement of these larvae. Research on abalone larvae has indicated that the settlement and metamorphosis of invertebrate larvae on coralline algae may be induced by a peptide, similar to the neurotransmitter gamma-aminobutyric acid (Morse, Hooker, Duncan & Jensen, 1979; Trapido-Rosenthal & Morse, in press). Further studies by Baloun & Morse (1984) have demonstrated that this may be inhibited or enhanced by altering the external concentrations of potassium ions.

While the mechanisms responsible for the settlement of *A. planci* larvae are poorly understood it is generally assumed that they settle in shallow water on reefs. This is because the few juveniles that have been found in the field have mostly been reported in these areas. Pearson & Endean (1969) discovered 46 juveniles (11–69 mm) in sheltered water (2–6 m depth) at Green Island on the Great Barrier Reef. They also found another 142 individuals (15–79 mm) at Fitzroy Island in a similar location. There are other reports of juveniles being found in the field; they, however, relate mainly to starfish which are bigger than 70 mm and could be small adults. More recently, numerous small juveniles (<50 mm) have been recorded by Moran, Bradbury & Reichelt (1985) on the Great Barrier Reef and by Zann (pers. comm.) in Fiji. One feature common to all reports is that the juveniles were located not only in shallow water but also a few years after an outbreak of adult starfish. Endean (1973b) considered that they may be the progeny of these adults and had been retained on the same reef as a result of water current patterns. If this is true then their occurrence in shallow water may be determined by the distribution and abundance of corals left after the initial outbreak of adults. Corals in shallower locations on reefs are commonly left by starfish (see p. 438). Perhaps the progeny of adults are distributed over a wide area of the reef, including shallow and deep water, but only those which settle in areas of high coral cover manage to change their diet, from algae to coral tissue, and survive. This does not, however, indicate where the starfish of initial outbreaks on reefs settle. If they normally settle in shallow water, it is strange that they are not seen until they are adults. Once they switch their diet to corals their presence on reefs becomes progressively more obvious with the increase in the size and number of feeding scars. One might presume that large numbers of smaller sized starfish (70–120 mm) would be reported more often if they settled initially in shallow water. If larvae become negatively buoyant prior to settlement as suggested earlier, then it is possible that the larvae responsible for the initial outbreaks on reefs may settle in deeper water at the base of reef slopes. More intensive searches of cryptic habitats in these areas on reefs prior to outbreaks may resolve this question.

PREDATORS

Twelve species of animals have been observed to feed on apparently healthy *A. planci*. These data have come from the field and the laboratory and are listed in Table VI. Predation of all four of the major stages in the cycle of *A. planci* (i.e. gametes, larvae, juveniles, and adults) have been reported.

Pearson & Endean (1969) have provided the only account of a damselfish (*Abudefduf curacao*) eating the eggs of a spawning starfish in the field.

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TABLE VI

Animals that have been observed to feed on A. planci

Type	Predator Name	<i>A. planci</i> stage predated	Reference
Anemone	<i>Stoichactis</i> sp.	Adults	Chesher, 1969a
Coral	<i>Pocillopora damicornis</i>	Larvae	Yamaguchi, 1973b; Ormond <i>et al.</i> , 1973
	<i>Pocillopora damicornis</i>	Juveniles	Yamaguchi, 1974b
Crab	<i>Promidiopsis dormia</i>	Adults	Alcala, 1974
	Xanthid	Juveniles	Lucas, 1975
Fish	<i>Abudefduf curacao</i>	Eggs	Pearson & Endean, 1969
	<i>Chromis dimidiatus</i>	Larvae	Lucas, 1975
	<i>Arothron hispidus</i>	Juveniles/Adults	Ormond & Campbell, 1974
	<i>Balistoides viridescens</i>	Juveniles/Adults	Ormond <i>et al.</i> , 1973
	<i>Pseudobalistes</i>	Juveniles/Adults	Ormond & Campbell, 1974;
	<i>flavimarginatus</i>		Owens, 1971
Gastropod	<i>Bursa rubeta</i>	Juveniles/Adults	Alcala, 1974
	<i>Charonia tritonis</i>	Juveniles/Adults	Endean, 1973b
Shrimp	<i>Hymenocera picta</i>	Juveniles/Adults	Wickler & Seibt, 1970; Wickler, 1973; Rainbow, 1974;
			Glynn, 1982a, 1984b
Worm	<i>Neaxius glyptocercus</i>	Juveniles/Adults	Brown, 1970
	<i>Pherecardia striata</i>	Juveniles/Adults	Glynn, 1982a, 1984b

Several studies have been conducted in the laboratory to investigate the predation of the eggs and larvae of *Acanthaster planci*. Yamaguchi (1973a) and Ormond *et al.* (1973) reported that larvae were eaten by corals. In addition, Yamaguchi (1974b, 1975) found that certain asteroid larvae and eggs, including those of *A. planci*, were either avoided or actively expelled by some species of fish. Experiments by Lucas (1975) demonstrated that while the larvae of *A. planci* were consumed by fish (Pomacentridae) they were not preferred and were discriminated against when there was a choice of larval species. These observations indicated that the larvae and perhaps eggs of *A. planci* contained substances that may repel predators.

This proved correct as Howden *et al.* (1975) managed to isolate toxic chemical compounds (saponins) from the eggs, ovaries, and body of *A. planci*. In a series of experiments Lucas *et al.* (1979) were able to show that these substances were partly responsible for the observed rejection of the eggs and larvae of *A. planci* by some species of fish. Those authors also observed that the fish varied in their discrimination and demonstrated that this may depend on the tastiness (*e.g.* whether the larvae and eggs are yolky or non-yolky) of the prey and also on the degree of hunger of the predator. Dana *et al.* (1972) have postulated that it is highly probable that predation of larvae in the field is extensive as the reef is composed of a vast array of plankton-feeders such as corals. Despite this claim they acknowledged that it was not known whether this type of predation was extensive.

Small juveniles of *A. planci* have been reported to be preyed upon in the laboratory by xanthid crabs (Lucas, 1975; pers. obs.). Yamaguchi (1974b) observed that they were badly damaged by the mesenteric filaments of

corals once they had attained adult morphology and changed their diet from algae. Several individuals were so severely damaged that they lost arm tips or complete arms. Most often these lost parts were regenerated within a few months. This type of damage was not recorded once the starfish had reached a sufficient size to avoid attack. These results highlight the fact that the mortality of starfish may be particularly high during the early stages just after metamorphosis. Indeed, it is possible that predation of young juveniles may be important in limiting the number of adult starfish on reefs.

A variety of other animals have been reported to feed on juvenile and adult *A. planci*. Endean (1969, 1977, 1982) proposed that the giant triton, *Charonia tritonis*, was a major predator of large juvenile and small adult starfish and was capable of altering their abundances in the field. This gastropod was reported to feed on *Acanthaster planci* by Pearson & Endean (1969). Using caged individuals they demonstrated that *Charonia tritonis* preferred starfish other than *Acanthaster planci* if given a choice. Indirect evidence from the field tended to support these findings. Of 28 tritons collected during two years of research on the Great Barrier Reef only seven regurgitated material associated with *A. planci*. An additional 12 tritons regurgitated parts of starfish, 11 of which were *Linckia* sp. and one was from *Culcita* sp. (Pearson & Endean, 1969). While appearing to prefer other starfish *Charonia tritonis* was also found to consume *Acanthaster planci* at a relatively slow rate. Pearson & Endean (1969) recorded that it ate only 0.7 starfish per week over a period of three months. Observations from Micronesia also suggested that attacks on *A. planci* by tritons were not always fatal and the animal was often able to escape and regenerate any damaged parts (Chesher, 1969a).

Another animal which has been proposed as a major predator of *A. planci* is the painted shrimp *Hymenocera picta* (Wickler, 1970; Wickler & Seibt, 1970). Experiments in aquaria indicated that this animal seeks out starfish using its antennules as chemoreceptors (Rainbow, 1974). The shrimp was observed to turn over small starfish and feed on their gonads and soft tissues (Wickler, 1970; Wickler & Seibt, 1970). One study indicated that this occurred only when *H. picta* was very hungry (Wickler, 1973). While these attacks caused the death of some individuals, Rainbow (1974) suggested that *H. picta* would not seriously injure adult starfish which were more than three times larger than the shrimp, but may affect juveniles. Therefore, he concluded that this shrimp was unlikely to control the abundance of adult starfish in the field. More recently, Glynn (1977) estimated the abundance of *H. picta* on lower fore-reef slopes in Panama and found that densities ranged from 1–118 individuals per hectare. From the results of field and laboratory studies he hypothesized that this shrimp was able to limit the abundance of *Acanthaster planci* as it was compelled to prey on it because of a lack of other more preferred starfish species (e.g. *Linckia* spp., *Nardoa* spp.). This produced a decrease in the rate of coral mortality in this area (see p. 417).

Four species of fish are known to feed on *A. planci*. This information comes from direct observations of predation or finding parts of *A. planci* in the stomachs of animals. Ormond *et al.* (1973) and Ormond & Campbell (1974) observed three species, *Arothron hispidus*, *Balistoides viridescens* and *Pseudobalistes flavimarginatus*, to feed on starfish in the Red Sea. By recording the frequency with which the remains of starfish (these were

considered to be unique for fish attacks) were sighted they estimated that approximately 200–800 adults were killed each year by these fish predators. This was thought to account for the gradual decline in starfish numbers which had been recorded over a two-year period. Predation by these species has not been reported to any great extent in other parts of the Indo-Pacific (e.g. Glynn, 1982a), although Wilson, Marsh & Hutching (1974) found spines and skeletal ossicles in the gut contents of a specimen of *Arothron hispidus* from the waters of Western Australia. Endean (1977) considered it unlikely that these species would be responsible for controlling starfish populations on the Great Barrier Reef since they were not common in this area. On the other hand, he maintained that the groper *Promicrops lanceolatus* was an important predator of large juvenile starfish on the Great Barrier Reef (Endean, 1982). He gave no real quantitative evidence to support this statement but he did report finding parts of juvenile starfish in the stomach of several specimens of this species (Endean, 1974, 1977). It is not, however, known whether the starfish were alive or dead when eaten. Indeed, Glynn (1984b) found that a variety of different animals including polychaetes, echinoids, crustaceans and fish fed on starfish which were either mutilated or dead. This activity was thought to hasten the rate of decomposition of these starfish.

So far, the only study to provide quantitative evidence of predation was that undertaken by Glynn (1982a, 1984b) in Panama. He found that starfish were often killed as a result of attacks by the shrimp *Hymenocera picta* and the annelid *Pherecardia striata*. Using a combination of laboratory and field experiments he demonstrated that 5–6% of starfish at any time were being preyed upon by *Hymenocera picta* and that 0.6% of individuals were being attacked by both predators. He used mortality and immigration rates to predict the abundance of starfish, which approximated that observed for this area over three years. From these results Glynn (1982a, 1984b) concluded that these two predators appeared to be responsible for preventing an increase in starfish numbers in the area studied.

There have been several other reports of animals preying on *Acanthaster planci* in the field (Chesher, 1969a; Brown, 1970; Alcalá, 1974) (Table VI). It is unlikely that any of these species would be important predators of this starfish given their biological characteristics. A further group of animals has been suggested as possible predators of *A. planci* but there is little or no evidence to support these assertions. They are: *Cassis cornuta* (Endean, 1969), *Cheilinus undulatus* (Endean, 1982), sharks (Dixon, 1969), *Murex* sp. (Chesher, 1969a), *Dardanus* sp. and *Cymatorium lotorium* (Ormond & Campbell, 1974).

At present there are little direct, quantitative data to suggest that predation plays an important role in limiting the numbers of starfish on reefs. There is some indirect evidence to suggest that juveniles and adults suffer extensive predation in the field. This comes from surveys, conducted in several parts of the Indo-Pacific, which have looked at the proportion of starfish with missing or regenerating arms and tissues. From these surveys it was found that from 17–60% of individuals in populations had suffered recent damage. The results of these surveys are given in Table VII. While the study of Glynn (1982a) demonstrated that the predation of juveniles and adults may be relatively high in the field there is little evidence to suggest that

TABLE VII

Proportion of starfish with missing or regenerating arms

Location	Proportion	Reference
Great Barrier Reef	26-60%	Pearson & Endean, 1969
Guam	43%	Glynn, 1982b
Hawaii	60%	Branham, 1973
Panama	17%	Glynn, 1982b
Papua New Guinea	50%	Pyne, 1970
Red Sea	30%	Ormond & Campbell, 1971
Western Australia	38%	Wilson <i>et al.</i> , 1974

it is important during the planktonic phase of *Acanthaster planci*. Results from laboratory studies have indicated that the eggs and larvae of this starfish may not be extensively preyed upon since they contain toxic saponins. Unfortunately, there are few data on the predation of these stages in the field. Until information is obtained many questions relating to the occurrence and propagation of outbreaks will remain unanswered.

ORGANISMS ASSOCIATED WITH *A. PLANCI*

Cannon (1972) listed a total of 34 organisms which were considered to be associated with *A. planci*. About five of these may have been duplicate records resulting from taxonomic errors. Another nine organisms were regarded as predators of *A. planci* while the association exhibited by many of the remaining organisms was uncertain. Eldredge (1972) presented a list of 15 organisms that were possibly associated with *A. planci*; at least six of these animals were known to be predators of this starfish.

A list has been prepared of those organisms which are known to be symbiotically associated with *A. planci*, are not predators of this animal and which have been identified taxonomically. This information is given in Table VIII. Besides the turbellarian, *Pterastericola* sp. all the other animals listed in Table VIII are regarded as commensal associates of *Acanthaster planci*. Little is known about the interrelationship between each of these animals and this starfish, although Cannon (1975) stated that the association between *Pterastericola* sp. and *Acanthaster planci* was a host-parasite one. As a result of his investigations into these organisms Cannon (1975) concluded that parasites and diseases were not significant determinants of starfish numbers as none could be found.

TABLE VIII

Animals found in association with A. planci

Copepod	<i>Onochopygus impavidus</i>	Humes & Cressey, 1958
	<i>Stellicola acanthasteris</i>	Humes, 1970
Fish	<i>Siphamia fuscolineata</i>	Allen, 1972; Eldredge, 1972
	<i>Carapus mourlani</i>	Cheney, 1973a
	<i>Encheliophis gracilis</i>	Cheney, 1973a
Polychaete	<i>Hololepidella nigropunctata</i>	Eldredge, 1972
Shrimp	<i>Periclimenes soror</i>	Hayashi, 1973
Turbellarian	<i>Pterastericola</i> sp.	Cannon, 1972, 1975

Recently, Lucas (1984) reported that starfish were subject to or affected by a disease while undertaking a series of laboratory experiments using a recirculating sea-water system. The spread of this disease could be checked with antibiotics, although sometimes individuals died after contracting this infection. Lucas (1984) described the early, advanced, and severe symptoms of this disease. The severe symptoms produced ulcerations and necrotic tissue and often led to the death of individuals several days after they had been observed. Coelomic fluid taken from infected starfish prior to the occurrence of necrosis was found to contain large numbers of bacteria. The disease was transmitted throughout the entire aquarium system.

The occurrence of this pathogen indicates a possible cause for the rapid disappearance of large aggregations which has been observed in the field (Moran, Bradbury & Reichelt, 1985). Experiments are at present in progress to isolate any pathogens which may possibly cause this (J. S. Lucas, pers comm.).

POPULATION DYNAMICS AND TAGGING

In ecology a group of individuals of the same type or species is referred to as a population. One thing that can be said in all certainty about populations is that they will fluctuate in size (Pielou, 1977). The study of the decrease and the increase of populations (population dynamics) has received great attention from both biologists and mathematicians. In essence, a population is thought of as a single entity which may be defined by a certain set of parameters. These parameters, which are similar for most populations, include; density, birth and death rates (*i.e.* natality and mortality), immigration and emigration rates, age distribution, growth rate of the population, dispersion and movement, longevity, size of individuals and sex ratio. A study of them can lead to a greater understanding of the ecology of a species, its relationship to the ecosystem and the reasons for its increase or decrease (Krebs, 1978).

There are few field data on the population dynamics of *A. planci*. One reason for this is that it is extremely difficult to recognize individuals in the field and follow them for long periods of time. O'Gower, McMichael & Sale (1973) stated that it has not been possible to undertake long-term field studies on *A. planci* due to the difficulties involved in tagging or marking starfish. Consequently, information relating to population parameters such as growth, longevity, mortality and movement is lacking. Up to the present time several tagging methods have been employed in a number of studies but they have proved largely unsuccessful. This problem does not relate solely to *A. planci* but is a problem common to echinoderms in general.

In the first studies which attempted to address this problem tags were attached through the body of starfish (Pearson & Endean, 1969; Branham *et al.*, 1971; Ormond & Campbell, 1974; Wilson & Marsh, 1975). This technique proved unsuccessful for a number of reasons. First, the starfish was able to release the tag by creating an opening in its body wall. Secondly, in some instances the starfish autotomized that part of the body (normally an arm) to which the tag was attached. Thirdly, some starfish became diseased and died. To overcome these responses, tags were tied around an arm or part of the oral disc using monofilament nylon or stainless steel wire (Pearson & Endean, 1969). This method also was unsuccessful as the star-

fish were able to extricate themselves from their harnesses. This technique has been tested on other types of starfish with little success (Kvalvagnaes, 1972).

Another method, reported by Roads & Ormond (1971), involved attaching coloured bands to the spines of starfish. This was carried out in a bid to follow the movement of starfish over a 24-hour period. While the method proved successful over this short time, experiments by Pearson & Endean (1969) demonstrated that the tagged spines would be shed within a few days.

Instead of attaching a marker to the body of a starfish several attempts have been made to recognize individuals by altering their external appearance. This has mainly involved clipping spines or removing arms. Cheney (1972a) and Ormond & Campbell (1974) clipped the spines of starfish as a means of following individuals in the field. Success was limited since the spines regenerate within a few months (Glynn, 1982b) and they are lost naturally from starfish (by way of predation) which may cause some confusion in identifying marked individuals. Consequently, this method of tagging is only useful for following a small population of starfish over a relatively short time (Vine, 1972).

Another method of marking individuals involved removing an arm or ray. Owens (1971) found that it took 116 days for a new arm to grow 10 mm and postulated that a medium sized individual may be recognizable for at least two years. Again this technique is of limited application and would be useful only for following a small number of starfish. As *A. planci* has a relatively small number of arms the number of starfish that are able to be individually marked is similarly small. Also, some uncertainty may arise when distinguishing between marked individuals in the field as a significant proportion have been observed to have missing or regenerating arms (see Table VII).

Aziz & Sukarno (1977) used natural external features (e.g. colour patterns, size, number of arms, position of broken spines) to identify starfish in the field. As the density of starfish was low, plastic markers were placed beside each animal to avoid mis-identifications. It is unlikely that this method would be suitable for studying starfish in outbreking populations as only a small number of features are used and they may not vary sufficiently between individuals to enable a large number of starfish to be identified (Glynn, 1982b).

Perhaps the most extensive series of experiments on tagging *A. planci* were those undertaken by Glynn (1982b) who tested several different methods including; branding with hot steel rods, applying dyes (Nile-blue sulphate solution, Neutral Red dye) to the arm and aboral surface, staining the aboral disc with saturated solutions of silver nitrate and iodine, inserting T-bar fasteners into the aboral disc, looping cable ties around arms, inserting stainless steel wire and monofilament nylon under the dermis, injecting India ink subcutaneously, inserting insulated wire through the disc and clipping spines. All these methods proved unsatisfactory with some producing death in animals. The staining, branding and dye techniques did not produce permanent, recognizable marks and the spines regenerated within four to five months. All tags which were attached to starfish were shed within one to two weeks.

Glynn (1982b) developed a technique for recognizing individual starfish in the field which consisted of using a series of natural characters which were more variable than those utilized by Aziz & Sukarno (1977). These characters included the natural arrangement and numbers of arms, madreporites, anuses, spines, and scars. Data relating particularly to the madreporites and anuses were selected to calculate a madreporite/arm code. Use of this code in conjunction with the other characters was shown in most instances to produce an individual descriptor for each starfish. As the coding process is relatively time-consuming this method would be unsuitable for following large numbers of animals (Glynn, 1982b). Given a small population of intransient starfish then this method, however, is useful and has the added advantages that the starfish are not handled extensively or subjected to injury which may result in changes in their biology, behaviour, and longevity.

DISTRIBUTION OF *A. PLANCI*

A. planci has been recorded throughout the Indo-Pacific region from reefs off the eastern coast of Africa to those in the Gulf of California and Panama. Whilst *A. planci* is known to be associated with coral reefs, it has not been observed on reefs in the Atlantic (Vine, 1973). The reason for this is not known. Predictions of catastrophe have been made should a sea level passage be constructed through central America joining the Pacific and the Atlantic. It has been suggested that this may lead to outbreaks of starfish in the Caribbean as a result of larval input from the Pacific (Johannes, 1971). There is no evidence to support this allegation.

The locations where *A. planci* has been observed in the Indo-Pacific are listed in Table IX and shown in Figure 6. Where this starfish has occurred at various locations within the same general area or territory they are listed under the one region (e.g. Great Barrier Reef, Mariana Islands). More specific information on the locations of starfish has been given where the reports are for isolated areas (e.g. Phuket). The reports themselves have been taken as much as possible from the scientific literature and the references from which these reports were obtained are given in the Table. This list of references is not exhaustive as those presented in the Table represent the major sources of information on starfish for that particular location. Areas where *A. planci* has been reported as "abundant" or "common" have been identified in the Table. For most locations an attempt has been made to define the period during which the starfish were observed. In some instances they were reported over several years at the one location (e.g. Ryukyu Islands) and in certain areas a second series of population increases have been observed (e.g. Great Barrier Reef) and these also have been noted.

Several conclusions can be made regarding the distribution of outbreaks of *A. planci* from the information contained in Table IX.

- (1) Not only have there been outbreaks on a wide variety of reefs throughout the Indo-Pacific region but they have occurred in isolated areas separated from other reefs by large distances of deep water; examples are the Hawaiian and Cocos-Keeling Islands, Wake Island, and Elizabeth and Middleton reefs.

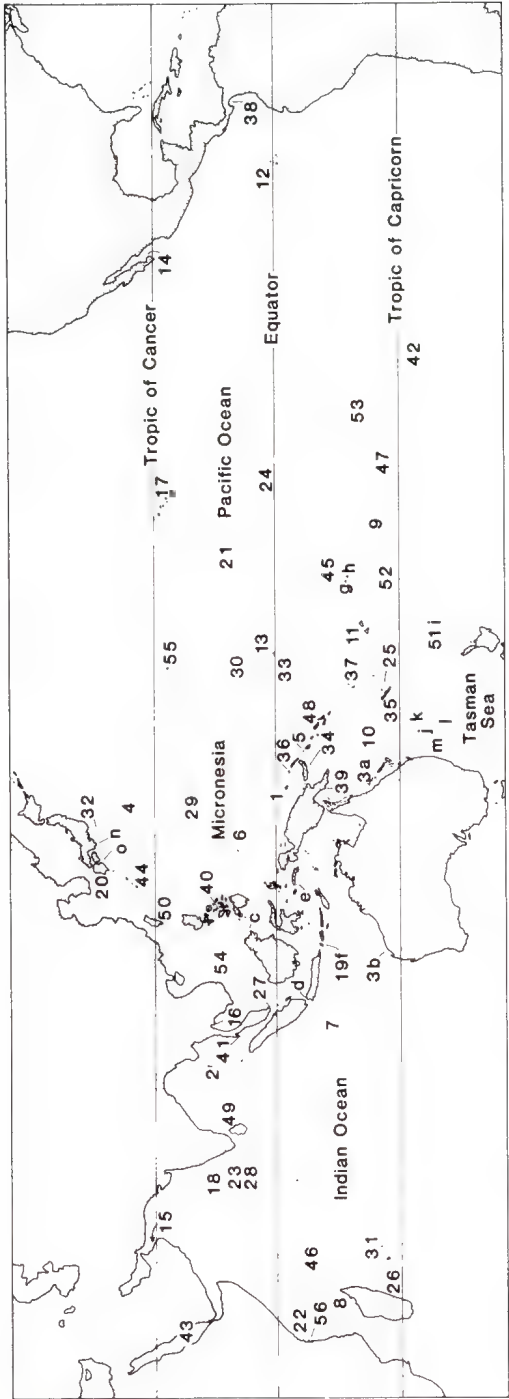


Fig. 6.—Distribution of *A. planci* in the Indo-Pacific region.

TABLE IX

*Distribution of A. planci in the Indo-Pacific region: the map numbers given refer to Figure 6: *starfish abundant or common; †second population increase*

Map No.	Location	Date	References
1	Admiralty Islands	1969*	Pyne, 1970
2	Andaman Islands	1953	Madsen, 1955
3	Australia:		
	a. Great Barrier Reef	1962-1977*, 1979†	Potts, 1981*; Kenchington & Pearson, 1982†
	b. Western Australia	1971-1974*	Wilson, 1972; Wilson & Marsh, 1974, 1975
4	Bonin Islands	—	Yamaguchi, 1977
5	Buka	1968*	Endean & Chesher, 1973
6	Caroline Islands	1969-1972*	Chesher, 1969a; Cheney, 1973b
7	Cocos-Keeling Islands	1949, 1976*	Clark, 1950; Colin, 1977*
8	Comoro Islands	1973*	Polunin, 1974
9	Cook Islands	1969-1970*	Devaney & Randall, 1973
10	Coral Sea:		
	Chesterfield Reef	1970	Endean & Chesher, 1973
11	Fiji	1969*, 1979†	Owens, 1969*, Robinson, 1971*; Zann, pers. comm.†
12	Galapagos Islands	1889	Sladen, 1889
13	Gilbert Islands	1969*	Weber & Woodhead, 1970
14	Gulf of California	1970*	Dana & Wolfson, 1970
15	Gulf of Oman	1982	Stanley, 1983
16	Gulf of Thailand	1973*	Piyakarnchana, 1982
17	Hawaiian Islands	1969*	Branham <i>et al.</i> , 1971
18	India:		
	Goa	1743	Vine, 1972
19	Indonesia:		
	c. Sabah	1967*	Yonge, 1968; Morris, 1977
	d. Pulau Pari Islands	1975*	Aziz & Sukarno, 1977
	e. Ambon Island	1973*	Soegiarto, 1973
	f. Bali	1982	Kenchington, pers. comm.
20	Japan:		
	n. Kushimoto	1973*	Hayashi & Tatsuki, 1975; Hayashi, 1975; Yamaguchi, in press
	o. Ashizuri-Uwakai	1972-1983*	Tada, 1983; Ito, 1984; Yamaguchi, in press
21	Johnston Islands	1969*	Chesher, 1969a
22	Kenya	1972	Polunin, 1974
23	Laccadive Islands	1976-1979	Sivadas, 1977; Murty <i>et al.</i> , 1979
24	Line Islands	1933	Edmondson, 1933
25	Loyalty Islands	1983	Conand, 1983
26	Madagascar	1958	Humes & Cressey, 1958
27	Malaysia	1968*	Chesher, 1969a
28	Maldiv Islands	1963	Clark & Davies, 1965
29	Mariana Islands	1967-1972*, 1979†	Chesher, 1969a*; Marsh & Tsuda, 1973*, Birkeland, 1982†
30	Marshall Islands	1969-1970*	Chesher, 1969a; Branham, 1971
31	Mauritius	1972*	Endean & Chesher, 1973; Fagoonee, 1985a
32	Miyake Island	1977-1980*	Moyer, 1978

TABLE IX (continued)

Map No.	Location	Date	References
33	Nauru	1971	Randall, 1972
34	New Britain	1968*	Endean, 1969
35	New Caledonia	1969* 1982	Chesher, 1969a; Conand, 1983
36	New Hanover	1968*	Pyne, 1970
37	New Hebrides	1970*	Endean & Chesher, 1973
38	Panama	1970*	Glynn, 1973, 1974
39	Papua New Guinea	1968-1970*	Pyne, 1970
40	Philippines	1972*	Beran, 1972
41	Phuket	1969*	Chesher, 1969a
42	Pitcairn Group	1970	Devaney & Randall, 1973
43	Red Sea	1968-1970*	Roads & Ormond, 1971
44	Ryukyu Islands	1957-1958*	Yamazato, 1969; Nishihira & Yamazato, 1972, 1973
		1969-1985*	Fukuda, 1976; Fukuda & Okamoto, 1976; Fukuda & Miyawaki, 1982; Matsusita & Misaki, 1983; Ui, 1985; Yamaguchi, in press
45	Samoa:		
	g. Western	1969-1970*	Garlovsky & Bergquist, 1970
	h. American	1977-1979*	Birkeland & Randall, 1979
46	Seychelles	1972	Endean & Chesher, 1973
47	Society Islands	1969-1971*	Chesher, 1969a; Devaney & Randall, 1973
48	Solomon Islands	1969-1971*	Garner, 1971
49	Sri Lanka	1971*	Vine, 1972; De Bruin, 1972; De Silva, 1985
50	Taiwan	1971*	Randall, 1972; Endean & Chesher, 1973
51	Tasman Sea:		
	i. Kermadec Islands	1978	McKnight, 1978
	j. Elizabeth Reef	1979, 1981*	McKnight, 1979; Veron, pers. comm.*
	k. Middleton Reef	1981*	Done, pers. comm.
	l. Lord Howe Island	—	Rowe & Vail, 1984a
	m. Solitary Islands	—	Rowe & Vail, 1984b
52	Tonga	1969*, 1976	Weber & Woodhead, 1970*; Francis, 1981
53	Tuamotu Archipelago	1970	Devaney & Randall, 1973
54	Vietnam	1981	Buznikov <i>et al.</i> , 1982
55	Wake Island	1969*	Randall, 1972
56	Zanzibar	1921	Caso, 1970

- (2) Some outbreaks have been recorded in areas of relatively high latitude; for example, Ashizuri-Uwakai, Kushimoto (Japan), Miyake Island (all between 33-34° N), and Elizabeth and Middleton reefs (approximately 30° S).
- (3) Most outbreaks have been over the same general period throughout the world. Major outbreaks were reported in many areas during the 1960s and 1970s (*e.g.* Great Barrier Reef, Ryukyu Islands and Micronesia). This synchrony of outbreaks was also apparent in the late 1970s with renewed population increases in several areas, notably the Great Barrier Reef, Guam and Fiji.

Major outbreaks involving large numbers of starfish and large scale coral destruction have occurred essentially in three areas in the Indo-Pacific region; the Great Barrier Reef, Micronesia, and the Ryukyu Islands. The first recorded outbreak of *A. planci* in the world was at Miyako Island in the Ryukyu Islands in 1957 (Nishihira & Yamazato, 1972). This was soon followed by reports of outbreaks in 1962 at Green Island on the Great Barrier Reef (Barnes & Endean, 1964), in 1967 at Guam in Micronesia (Chesher, 1969a) and in 1969 on the west coast of Okinawa approximately 320 km to the north of Miyako Island (Nishihira & Yamazato, 1972). Outbreaks have occurred continually in the Ryukyu Islands over the last 15 years (Yamaguchi, in press) leading to large scale control efforts. Soon after they were reported in Micronesia extensive surveys were undertaken to determine the extent of the starfish populations and the coral damage caused by them (Chesher, 1969a). Large populations of *A. planci* have also been recorded in the Red Sea, Fiji, Panama, Samoa, and the Cook Islands. The Hawaiian Islands also experienced outbreaks of *A. planci* towards the end of the 1960s; they appeared, however, to have little effect on the coral communities in this area (Branham *et al.*, 1971).

OUTBREAKS OF *A. PLANCI*

DEFINITION OF OUTBREAKS

It has come to be realized that outbreaks are not all the same but are highly variable phenomena. Despite this variability, attempts have been made to define what is meant by outbreaking and normal populations of *A. planci*. These definitions are important when trying to compare the populations on different reefs and summarize the extent of the phenomenon. As the definitions were derived using a variety of survey techniques, in general they cannot be directly compared and consequently a standardized definition for the two population states has not been formulated. The various definitions proposed are given in Table X. All of those listed define outbreaking and

TABLE X
Definitions of an outbreaking and normal reef

Definition	Reference
Outbreaking	
14 starfish per 1000 m ²	Endean & Stablum, 1975b
40 starfish per 20 min swim	Pearson & Endean, 1969
100 starfish per 20 min. swim or manta tow	Chesher, 1969a
10 starfish per 1 min spot check	Pearson & Garrett, 1976
Normal	
About 1 starfish per 100 m ² of reef	Dana <i>et al.</i> , 1972
About 6 starfish per km ² of reef	Endean, 1974
Between 4-5 starfish per km of reef	Chesher, 1969a
Between 5-20 starfish per km of reef	Ormond <i>et al.</i> , 1973
Less than 14 starfish per 1000 m ²	Endean & Stablum, 1975b
Less than 10 starfish per 20 min swim	Pearson & Endean, 1969
Less than 20 starfish per 20 min swim	Chesher, 1969a

normal reefs in terms of the number of starfish observed over some unit of the survey. As discussed earlier, this is a difficult task since starfish may not be distributed evenly over reefs. Furthermore, their cryptic behaviour and colour make them difficult to observe in the field, particularly when the reef structure is patchy (Kenchington & Morton, 1976). Chesher (1969a) defined several types of populations which he considered to be "normal". In analysing this data, Dana, Newman & Fager (1972) concluded that very few populations met Chesher's criteria and that the definitions for outbreaking and normal populations were inadequate. Dana and his colleagues based their conclusions on the following information obtained from the surveys conducted in Micronesia.

- (1) Outbreaks were not evenly distributed on reefs.
- (2) The populations varied temporally.
- (3) There were different types of outbreaks each with continuously varying densities of starfish.
- (4) Some large outbreaks caused little coral mortality.

Kenchington & Morton (1976) considered that it was not possible to define a normal population since little was known about the rôle of *A. planci* in the ecology of the reef. It would appear from these opinions that there is no real solution to this problem and that the terms "outbreak" and "normal" will continue to be defined in such imprecise terms until more is known about the ecology of *A. planci* and a standard method of survey is adopted. Such a survey should include not only data on the abundance of the predator but also that of the coral prey as the two are inextricably linked. More accurate descriptions of starfish populations may also be obtained if the extent of these abundances was presented in some standardized manner. Without a doubt Potts (1981) was correct when he stated that "outbreaks cannot be recognized by any single qualitative or quantitative character" (p. 66).

PRIMARY AND SECONDARY OUTBREAKS

Often outbreaks are classified into two types, primary and secondary (Potts, 1981). In essence, primary outbreaks involve increases in starfish abundance that are associated with the changes in certain local factors in and around reefs and have not arisen from nearby populations (Endean, 1973b; Potts, 1981). On the other hand, secondary outbreaks have been defined as those which have resulted from nearby outbreaks either due to larval input from areas of primary outbreaks or by adult migration (Endean, 1973b). This distinction is relatively clear cut but it is not a simple task to classify outbreaks on this basis since it requires some knowledge about the processes which have lead to their existence. Often it is not possible to determine whether an outbreak is primary or secondary as little quantitative data are available concerning these processes. Primary outbreaks have been demonstrated by implication rather than by direct evidence. Their existence has been inferred particularly in areas isolated by large distances of deep water, such as some of the reefs in Micronesia. It is an extremely remote possibility that outbreaks could have originated in these areas due to input of larvae or adults from other areas and it has been

assumed that they arose in response to changes in local conditions. While primary outbreaks may have occurred in these essentially simple reefal systems it is much more difficult to demonstrate their existence on reefs which are large and heterogeneous in structure, such as the Great Barrier Reef. In this instance, primary outbreaks are difficult to infer since the reef is not one single structure but is composed of a multitude of individual reefs which are separated by relatively short distances of shallow water (about 60 m deep). Outbreaks on them may arise both as a result of changes in local factors or due to larval input or adult migration. Unfortunately, there do not appear to be any differences in the manner in which these outbreaks occur which would enable them to be readily identified. One possible way of determining where primary outbreaks have taken place is to ascertain where outbreaks are likely to have begun. In hindsight, this might be accomplished by obtaining information on the pattern and extent of outbreaks over these large complex reefal systems. From this type of information Kenchington (1977) proposed that primary outbreaks were present on the Great Barrier Reef in an area just to the north of Green Island during the late 1950s (see p. 434). These outbreaks were thought to have triggered a wave of secondary outbreaks which moved increasingly southwards. While this model parallels observations on the Great Barrier Reef for that period, unfortunately there are few data to indicate where primary outbreaks originated, despite numerous surveys. Ebert (1983) has suggested an alternative explanation for the pattern of outbreaks recorded. He proposed that the apparent southward movement in the centre of outbreaks may be the result of differential growth of starfish in areas of varying latitude or temperature. Ebert (1983) further postulated that this movement may stem from one major primary outbreak or a series of simultaneous primary outbreaks. While this alternative model would seem plausible, there is insufficient evidence to indicate that variations in the growth rates of starfish in different latitudes would be large enough to account for outbreaks occurring at least a decade apart.

Potts (1981) suggested that the Great Barrier Reef was probably the only area in the world where extensive secondary outbreaks have occurred. Information given by Yamaguchi (in press) now suggests that outbreaks of similar magnitude and type have also taken place in the Ryukyu Islands. Primary outbreaks were thought to have occurred in this region during 1953–1957 (Potts, 1981). A further series of extensive outbreaks (which are still occurring) took place after that time throughout this region and were first reported in Okinawa in 1969. It is not clear whether they arose from new primary outbreaks or whether the outbreaks originated from those which were present in the late 1950s. Those recently reported on mainland Japan and at Miyake Island were considered to represent secondary outbreaks (Yamaguchi, in press).

Outbreaks of *A. planci* have occurred in a similar manner on the Great Barrier Reef and in the Ryukyu Islands. Both regions have experienced extensive secondary outbreaks that have been extremely prolonged. They have been occurring intermittently in these regions for the last 25 years at least. This may be partly related to their structure. As mentioned earlier both areas are composed of many reefs separated by relatively short distances of water, which are often shallow. As the reefs in these areas are

close to one another then the chance of large-scale recruitment to some reefs is likely to be high. This is based on the assumption that larvae coming from a nearby reef upstream would be less diluted than those from reefs separated by large distances of water. In some instances where reefs are separated by narrow, shallow channels of water there is also the potential for outbreaks to be perpetuated by adults immigrating from nearby areas (Endean, 1973b). These mechanisms may lead to a higher proportion of reefs being affected by outbreaks and they may also result in the development of chronic outbreaks on some reefs. Thus, there may be a greater potential for reefal complexes such as the Great Barrier Reef and the Ryukyu Islands to suffer protracted outbreaks than reefs isolated by deep water and long distances. This may also depend on a variety of other factors (e.g. water currents) which are poorly understood, but it is clear that care must be taken when deciding whether an outbreak (primary) has arisen *de novo* (Potts, 1981) or as a consequence of other mechanisms (secondary). Presumably, this distinction will become clearer when more is known about the causes of outbreaks.

POPULATION MODELS

Until recently, very few mathematical models had been developed as a means of identifying some of the major processes underlying the *Acanthaster* phenomenon. Perhaps this deficiency reflects the lack of suitable information for such modelling procedures. To date, two types of models have been developed and both focus on the interaction between the starfish predator and its coral prey. This was first attempted by Antonelli & Kazarinoff (1984) who considered the interaction representative of that between a herbivore and vegetation. The aggregative behaviour of *A. planci* was incorporated into this model by employing a quadratic co-operative term. This mathematical term was responsible for producing stable limit cycles. The interaction that was modelled was that between two types of corals and one starfish. Two important aspects of the model were the aggregative behaviour of the starfish and the preference shown by the starfish towards its prey. The stability of this interaction was analysed using Hopf bifurcation theory. If no preference was demonstrated by the starfish then the model was found to be "neutrally" stable. The model, however, exhibited stable limit cycle behaviour as the starfish began to prefer one coral over another. The stability of these limit cycles was found to strengthen as coral preference became more asymmetric. As they had demonstrated that natural mechanisms could be responsible for cyclic fluctuations in populations of *A. planci*, Antonelli & Kazarinoff (1984) hypothesized that outbreaks may be natural phenomena akin to those observed in other herbivore-plant interactions.

Bradbury, Hammond *et al.* (1985a) questioned whether the asymmetry used by Antonelli & Kazarinoff was appropriate. They constructed a model from qualitative data on the abundance of starfish and corals from a number of reefs on the Great Barrier Reef. When combined, these data produced a composite view of the interaction. By considering the topological properties of this interaction they demonstrated the existence of cycles that were argued to be the qualitative analogues of stable limit cycles.

Four distinct phases were identified from this qualitative interaction between *A. planci* and corals; (1) coral phase (where coral cover is at a maximum and few starfish are present); (2) outbreaking phase (where the corals are diminishing in abundance and the starfish are rapidly increasing in number); (3) Crown-of-thorns phase (where coral abundance is at a minimum and starfish numbers are at a maximum); and (4) recovery phase (where coral cover is once again increasing and the abundance of crown-of-thorns has declined). These phases reflect the sorts of changes in the abundance of starfish and corals which have been observed in the field. The stability of this cycle was inferred rather than analytically derived since it was demonstrated on reefs whose coral communities were structurally dissimilar. Bradbury *et al.* (1985a) considered that the qualitatively stable cycles may be driven by endogenous factors (forces operating from within the interaction), such as delays in the interaction which may occur due to the structure of the reef. They suggested that this was a more important asymmetry in their model than that employed by Antonelli & Kazarinoff (1984). They postulated that the cycles may also be driven by exogenous factors (forces acting on the interaction from outside) (*e.g.* terrestrial run-off, predation) which may prevent the cycle from heading towards a stable point or level.

Bradbury, Hammond, Moran & Reichelt (1985b) extended this model to include data on starfish and coral abundances that had been collected on each of two occasions in one year at each of almost 100 reefs on the Great Barrier Reef. They once again utilized the qualitative aspects of the data to observe the underlying processes in the interaction. In doing so, they employed the principles of graph theory to plot values for each reef as discrete points in a lattice of two dimensions. The axes of this lattice corresponded to predator and prey abundance categories. This technique revealed three types of dynamic behaviour in the interaction; stable points, stable cycles, and chaos. Their existence had been defined in earlier models of predator-prey interactions (May, 1975). Unlike the earlier studies, the results of Bradbury *et al.* (1985b) indicated that these three states may occur at the same time within the one interaction. Consequently, they argued that the interaction may be a result of endogenous forces that stem from differences in the life history of the predator and its prey.

While the results of these studies are of interest they create a simplistic representation of the phenomenon. At present these models can be considered in their infancy and no doubt they will become increasingly sophisticated as more accurate biological and ecological information becomes available.

ACANTHASTER OUTBREAKS ON THE GREAT BARRIER REEF

INTRODUCTION

The Great Barrier Reef is the largest reefal system in the world, comprising of some 2500 individual reefs and extending along almost the entire Queensland coast of Australia for a distance of about 2000 km (Great Barrier Reef

Marine Park Authority, 1981). This section which deals specifically with outbreaks on the Great Barrier Reef has been included for the following reasons.

- (1) Outbreaks which have occurred in this region are probably the most extensive in the world having been reported in an area from the Swain reefs to those near Princess Charlotte Bay (see Fig. 7), a distance of about 1200 km.
- (2) With the possible exception of the Ryukyu Islands, the Great Barrier Reef is thought to be the only place in the world where secondary outbreaks have occurred (Potts, 1981).
- (3) Two series of extensive outbreaks, the second occurring at present, have taken place on the Great Barrier Reef and they are probably the most well documented of the outbreaks that have been reported in the Indo-Pacific region. Extensive scientific surveys have been undertaken on the Great Barrier Reef for almost 20 years providing the most accurate account of starfish outbreaks to date. The only other place where extensive surveys have been undertaken is in Micronesia and these were conducted in the late 1960s and early 1970s. No major surveys have been undertaken in the Ryukyu Islands apart from that reported by Nishihira & Yamazato (1972) at Okinawa. Most efforts in this area have been directed towards undertaking control programmes.

The information presented in this section provides an excellent example of the way in which outbreaks may develop in large reef systems. This information will also be used to discuss the pattern of outbreaks and the problems associated with attempts to determine the extent of these phenomena.

Outbreaks of the crown-of-thorns starfish were first recorded on the Great Barrier Reef in 1962 at Green Island. It has been reported that large numbers of starfish were observed before this time during 1954 on Lodestone reef and 1957 in the Swain reefs but such observations remain unsubstantiated (Vine, 1970; D. Tarca, pers. comm.). Outbreaks continued until 1977 and then for a period of over two years no reports were received. At the end of 1979 new outbreaks were once again reported at Green Island. It is not known whether outbreaks were present on the Great Barrier Reef between 1977 and 1979 or whether this reflects the fact that no scientific surveys were undertaken during this period. Despite this, for convenience, the following account of outbreaks on the Great Barrier Reef has been divided into the two periods; those that occurred between 1962 and 1977 and those reported from 1979 to the present. Information about outbreaks in most instances has been drawn from the results of both published and to a lesser degree, unpublished scientific surveys. The extent and duration of these surveys are given in Figure 7.

OUTBREAKS: 1962-1977

Large numbers of *A. planci* were recorded at Green Island in 1962 (Barnes & Endean, 1964). Over the next two years they increased to plague proportions which resulted in the loss of almost 80% of the live coral on

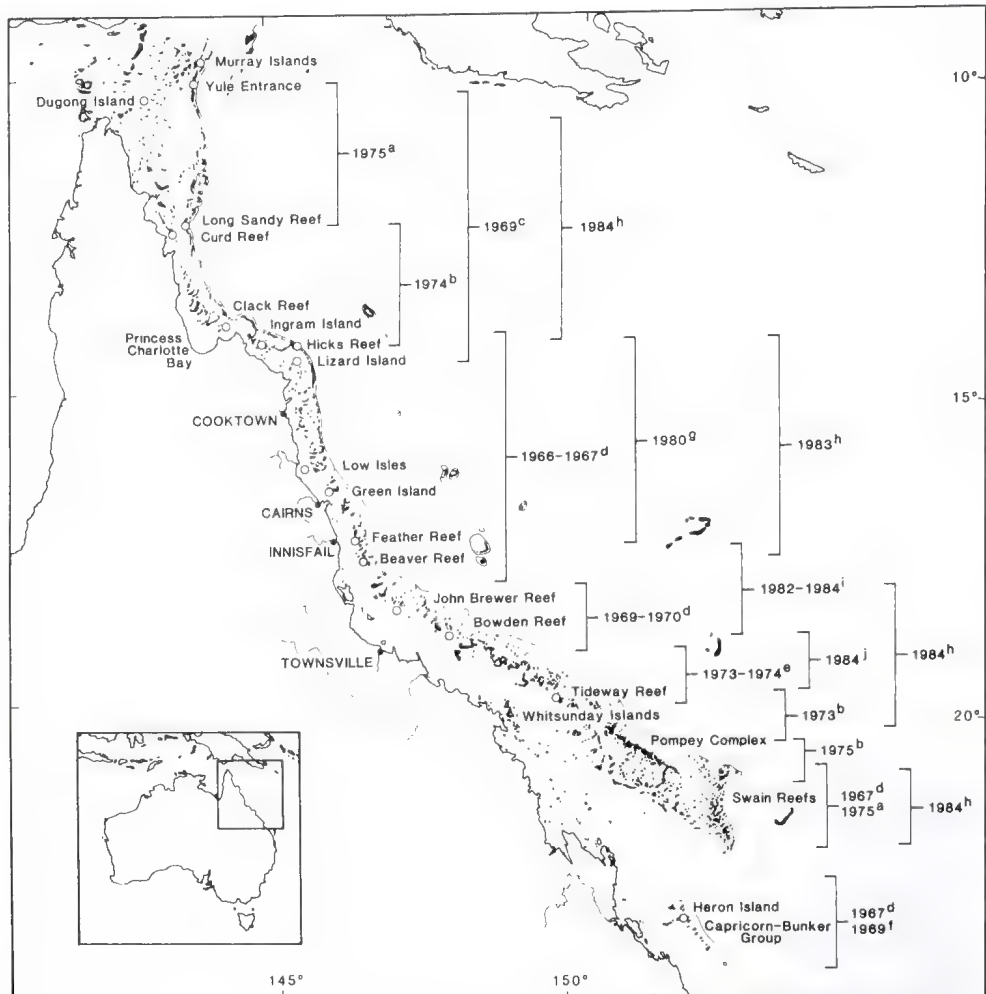


Fig. 7.—Major crown-of-thorns surveys carried out on the Great Barrier Reef: a, Pearson & Garrett (1978); b, Pearson & Garrett (1976); c, Vine (1970); d, Pearson & Endean (1969); e, Morton (1975), Endean & Stablum (1975a), Pearson & Garrett (1975), Kenchington (1975a,b; 1976), Kenchington & Morton (1976); f, Pearson (1972b); g, Nash & Zell (1982); h, Great Barrier Reef Marine Park Authority (unpubl. data); i, Hegerl (1984b); j, Great Barrier Reef Marine Park Authority (1985).

that reef (Pearson & Endean, 1969). The population on Green Island persisted until about 1967 as few starfish were observed after this time (Endean, 1974). Barnes (1966) has given a detailed description of the movement of this population and its effects on the coral communities on the reef. Since this outbreak had such a catastrophic effect on the corals at Green Island evidence of large populations was sought in other areas of the Great Barrier Reef. Throughout the next decade a number of surveys were carried out to determine the extent of these outbreaks (Fig. 7).

By 1966 many of the inner platform reefs between Michaelmas Reef (near Green Island) and Beaver Reef were found to carry large populations of starfish (Pearson & Endean, 1969; Endean, 1974), while there were very few

starfish on reefs to the south (Endean & Stablum, 1973b). In 1966 to 1967 outbreaks were beginning to appear on the reefs off Innisfail (Pearson, 1974) and some reefs even further to the south (e.g. Otter and Rib Reefs) (Endean & Stablum, 1975b). Coral destruction on many of these reefs, particularly Feather and Peart, was estimated to have exceeded that at Green Island (Pearson, 1974). By 1969 their populations had diminished to low levels (Pearson, 1981).

Surveys conducted from 1966 to 1968 showed that reefs as far north as Lark Reef (just north of Cooktown) had large numbers of *A. planci* (Pearson & Endean, 1969; Endean & Stablum, 1973b). For example, the reefs around Low Isles were noted to have many *A. planci* on them in 1966 and 1967 (Pearson & Endean, 1969). In 1968, none were observed in a survey of 21 reefs in the northern section of the Great Barrier Reef, from Lizard Island to Thursday Island (Vine, 1970). Surveys of Lizard Island and nearby Carter Reef in 1973 revealed few starfish and little coral mortality (Endean, 1974).

Many of the reefs off Townsville (e.g. Slashers, Britomart, John Brewer, Lodestone, and Trunk) were found to possess large populations of *A. planci* (Kenchington, 1975a) by 1970. Prior to this, starfish had been very rare on these reefs (Kenchington, 1975a, 1976). Several reefs, particularly John Brewer, were extensively damaged during this period (Pearson, 1981). The starfish populations on reefs in this region had begun to decline substantially by 1971 (Endean & Stablum, 1973b). Starfish outbreaks were recorded on several reefs further to the south (e.g. Bowden, Mid, Prawn, Shrimp and Shell) during 1972 to 1973 (Endean, 1974) and 1973 to 1974 (Kenchington, 1975a,b, 1976). These same reefs did not have starfish aggregations on them in 1970 (Endean & Stablum, 1973b; Pearson & Garrett, 1976). At the same time some reefs even further south had experienced outbreaks (e.g. Hope, Gould, Rafter, and Line) while others in between had not (e.g. Stanley, Old, and the Darley complex) (Endean & Stablum, 1973b). By 1973 the southernmost extent of these outbreaks was thought to be at Tideway Reef (Pearson & Garrett, 1975).

Increasing numbers of starfish were reported on several reefs in the Swain complex during 1973 to 1974 (Pearson & Garrett, 1976). Previously only one starfish had been recorded in this region during a survey of several reefs in 1967 (Endean, 1969). Surveys conducted during 1975, however, found outbreaks of starfish on a number of reefs in the northeastern sector of the Swain complex (Pearson & Garrett, 1976). Extensive coral mortality was also observed on these reefs.

While starfish outbreaks had been recorded during this time on reefs in the Swain complex they had not been reported on reefs immediately to the north in the Pompey complex. Surveys undertaken in 1975 failed to locate any evidence of starfish outbreaks in this area (Pearson & Garrett, 1976). During the 1960s and 1970s no major outbreaks were recorded on reefs to the south in the Capricorn-Bunker Group. Small populations of adult starfish were recorded in the lagoons on some reefs (e.g. Llwelllyn Reef, Lady Musgrave Island) during 1967 and 1969 although they appeared to be causing minimal coral mortality (Pearson, 1972b). These were thought to be "resident" populations in equilibrium with the surrounding coral communities.

Surveys in the northern sections of the Great Barrier Reef in 1974 found evidence of outbreaks of *A. planci* at Clack Reef and Ingram Island near Princess Charlotte Bay. No evidence of starfish outbreaks was, however, recorded north of this area (to Curd Reef) during this time (Pearson & Garrett, 1976). Towards the end of 1975, abnormal amounts of coral mortality were found on reefs between Long Sandy Reef and Dugong Island (north of Cape York). This damage was attributed to the crown-of-thorns starfish despite the fact that very few were observed and the damage was not recent (Pearson & Garrett, 1978). There is no direct evidence to suggest that major outbreaks have occurred north of Princess Charlotte Bay, although two localized aggregations of starfish were reported in the Torres Strait at the Murray Islands in 1975 (Hegerl, 1984a) and Yule Entrance in 1974 (Pearson & Garrett, 1976) (Fig. 7). By 1977, the only known large populations of *A. planci* were restricted to the eastern section of the Swain Reefs (Kenchington & Pearson, 1982).

OUTBREAKS: 1979-1985

No outbreaks were recorded after 1977 on the Great Barrier Reef for almost two years, perhaps because major scientific surveys were not conducted during this period. From late 1979 to early 1980 another large population of starfish was, however, observed at Green Island (Kenchington & Pearson, 1982). By December 1979, it was estimated that approximately 60% of hard corals had been killed and the starfish population comprised between 350 000 and 2 000 000 individuals (Endean, 1982). Some two months later almost 90% of the live hard coral cover on Green Island had been killed and by the end of the year the starfish population had declined dramatically (Endean, 1982). As a consequence, surveys were renewed in a bid to locate further large populations of *A. planci* (Fig. 7).

Four reefs between Hicks Reef and Ellison Reef (near Beaver Reef; Fig. 7) were found to carry large starfish populations on them in early 1980, while several others exhibited recent coral damage (Nash & Zell, 1982). By 1983 *A. planci* was observed on 23 reefs in this region, although only two reefs were considered to have had large populations of this starfish (Great Barrier Reef Marine Park Authority, unpubl. data). An additional five reefs were considered to have low coral cover which was presumed to be due to *Acanthaster* predation. Towards the end of 1984, 24 mid-shelf reefs in this region were found to have extensive areas of dead coral which was attributed to *Acanthaster* predation (Great Barrier Reef Marine Park Authority, 1985). Although few starfish were seen on these reefs large numbers were recorded on several of the ribbon reefs east of Lizard Island (Hegerl, 1984b). Just prior to this, surveys were conducted on reefs to the north, from Princess Charlotte Bay to Whyborn Reef near the tip of Cape York. No evidence of recent outbreaks was found (Hegerl, 1984b).

During 1983 and 1984 (approximately four years after the start of the outbreak on Green Island) outbreaks were observed on a number of reefs near Townsville (Bradbury, Done *et al.* 1985; Bradbury *et al.*, 1985a). Nineteen of 42 reefs in the central section of the Great Barrier reef were reported to have *Acanthaster* on them during surveys conducted in late 1984. Of these 19, only 12 had large numbers of starfish on them and nearly

all were mid-shelf reefs located near Townsville (Great Barrier Reef Marine Park Authority, unpubl. data). Surveys conducted to the south of this region during 1983 and 1984 on reefs east of the Whitsunday Islands, in the Pompey and Swain complexes and the Capricorn-Bunker group failed to find any evidence of outbreaks (Great Barrier Reef Marine Park Authority, unpubl. data, 1985). It would appear that by the middle of 1985, the southern and northern limits of this second series of outbreaks were to be found at reefs near Townsville and Lizard Island, respectively.

PATTERN OF OUTBREAKS

It has been suggested on numerous occasions that outbreaks moved in a southerly direction during the 1960s and 1970s (Talbot & Talbot, 1971; Pearson, 1972b; Endean, 1974). In addition, Kenchington (1977) suggested that this pattern was initiated by primary outbreaks that had occurred on reefs to the north of Green Island in the mid 1950s. While there is evidence to support the notion that outbreaks tended to be in more southerly latitudes with time there are a number of inconsistencies in this model. First, there is no direct evidence that primary outbreaks were present on reefs north of Green Island in the 1950s. In fact, outbreaks were observed on many reefs in this region during 1966–1968 (Pearson & Endean, 1969). Secondly, a consistent southward trend in the pattern of outbreaks is not evident. For example, Rib Reef (located just north of Townsville) had a large population of starfish on it in 1966 several years before the majority of reefs in this area and at a time when reefs further north off Innisfail were only just beginning to experience them. Similarly reefs such as Hope, Gould, Rafter and Line were observed to have outbreaks in 1972 and 1973 at the same time as those much further to the north (*e.g.* Bowden, Prawn, and Shrimp). Those at the southern end of the Great Barrier Reef in the Swain region also were experiencing outbreaks during this period despite the fact that a vast area of reefs further to the north (Pompey complex) were not (Birtles *et al.*, 1976).

While some of these anomalies may be due to inadequate data it is clear that the southward movement model proposed by several authors provides only a general description of the pattern of outbreaks in the 1960s and 1970s. Indeed, it is possible that this model is derived in part by the fact that the surveys themselves moved in a southerly direction with time (Fig. 7). Most important, however, the model cannot be applied to the entire Great Barrier Reef since it relates only to those reefs in the southern half of it (*i.e.* reefs south of Green Island).

The results of surveys completed since 1979 tend to support the notion of a general southward movement of outbreaks as reefs off Innisfail experienced them in 1981 and 1982 (some two years after those at Green Island) and those off Townsville in 1983 and 1984. If this pattern continues then reefs between Townsville and the Whitsunday Islands will outbreak over the next few years. During this time surveys need to be undertaken repeatedly on reefs to provide a more accurate description of the movements of outbreaks in this region.

Only one attempt has been made to analyse the large volume of information collected during surveys conducted over the last 20 years. In this

study starfish abundances, recorded on reefs throughout the Great Barrier Reef between 1979 and 1984, showed a strong temporal component in the pattern of outbreaks rather than a spatial one (Bradbury, Done *et al.*, 1985). From the analysis it was concluded that this indicates "some sort of long-term cyclicity at the whole GBR scale" (Bradbury, Done *et al.*, 1985, p. 108). While this may be true it does not invalidate the southward movement model which relates to the pattern of outbreaks occurring over a completely different scale (*i.e.* reefs south of Green Island). More analyses of this type are needed if realistic models of the *Acanthaster* phenomenon are to be achieved. In order to do this a more homogeneous data set is, however, needed (Bradbury, Done *et al.*, 1985).

No general pattern in the occurrence of outbreaks can be readily discerned for reefs to the north of Green Island. This is partly because the region is more remote and was surveyed less intensively than reefs in the southern half of the Great Barrier Reef. Large numbers of starfish were recorded on several reefs as far north as Lizard Island during 1966 and 1967. By 1974 they were observed further north near Princess Charlotte Bay and extensive areas of dead coral were reported on reefs near Cape York in 1975. It is not known whether these observations reflect either a northward movement in the outbreaks or indeed the surveys, or whether they suggest the occurrence of earlier primary outbreaks. Repeated surveys of reefs in this region during the next few years may provide a more accurate picture of the pattern of spread of these outbreaks.

There are two other interesting features relating to the pattern of outbreaks on the Great Barrier Reef that should be mentioned.

(1) No outbreaks have been observed in the Capricorn-Bunker Group at the far southern end of the Reef. Surveys during the late 1960s did not find any evidence of outbreaks although small resident populations of starfish were reported in sheltered locations on some reefs (Pearson, 1972b). Since that time no evidence of outbreaks has been reported on these reefs (Done, Kenchington & Zell, 1982; Great Barrier Reef Marine Park Authority, 1985). Lucas (1973, 1975) has suggested that outbreaks may not occur in this region as the temperature regime is less favourable for the survival of large numbers of larvae. This would seem unlikely, however, as outbreaks occurred on reefs nearby in the Swain region and were also observed on Elizabeth and Middleton Reefs (Table IX, see p. 424) which are located approximately 850 km to the southeast.

(2) Certain reefs appear to be more susceptible to outbreaks than others. Recent information has indicated that 16 of 21 reefs that had large numbers of *A. planci* in 1983 also had outbreaks on them during 1966 to 1970 (Great Barrier Reef Marine Park Authority, 1984a). Of these reefs several mid-shelf reefs between Cairns and Townsville have experienced catastrophic outbreaks on both occasions which involved large numbers of starfish and resulted in extensive coral mortality. Outbreaks of this sort were experienced on Green Island (Pearson & Endean, 1969), Feather (Pearson, 1974), Rib (Pearson & Endean, 1969), and John Brewer (Pearson, 1981) reefs from 1960 to 1970. These same reefs suffered outbreaks of a similar magnitude between 1979 and 1985 (Endean, 1982; Hegerl, 1984b).

In contrast some reefs, particularly those on the outer edge of the continental shelf, do not seem to be susceptible to outbreaks. For example,

only one outer barrier reef was recorded to have large numbers of starfish on it during surveys conducted between 1966 and 1969 (Pearson & Endean, 1969; Pearson, 1970). In addition, some outer shelf reefs (e.g. Myrmidon Reef located off Townsville) have never been reported to have suffered an outbreak (Endean & Stablum, 1975b; Great Barrier Reef Marine Park Authority, unpubl. data). On the other hand, mid-shelf reefs appear to have a higher incidence of outbreaks. Almost all those surveyed off Townsville during 1984 were found to have large numbers of starfish (Hegerl, 1984b; Great Barrier Reef Marine Park Authority, unpubl. data). There are inconsistencies, however, as some reefs in this region (e.g. Wheeler and Davies) had few starfish on them during the 1970s despite being situated close to reefs (John Brewer, Lodestone, and Keeper) that had large outbreaks (Endean & Stablum, 1975b). Why some reefs should be more likely to experience an outbreak than others is not understood. Perhaps factors such as the morphology and position of reefs, water currents, temperature, and salinity are important in determining the "outbreak behaviour" of individual reefs. These factors may operate on both the adult and larval stages of the life cycle of *A. planci*.

EXTENT OF OUTBREAKS

Information on outbreaks of *A. planci* over the last 20 years has been compiled by the Great Barrier Reef Marine Park Authority. This information is based on reports of the presence or absence of starfish not only from scientific surveys but also other reef users (e.g. sport divers, tourist operators). Up until 1983 reports dating from 1957 had been compiled for 516 reefs or approximately 20% of the total number of reefs comprising the Great Barrier Reef system (Great Barrier Reef Marine Park Authority, 1984a; Kenchington, 1985). A summary of the information received for 1984 indicated that *A. planci* was not observed on 57% of the 178 reefs for which reports were received. It was deemed to be uncommon (<10 starfish observed) on 18% of reefs and common (10–39 starfish observed) on a further 9% of reefs. Aggregations of 40 or more starfish were reported on the remaining 16% of reefs (Great Barrier Reef Marine Park Authority, 1984b).

Despite the large amount of information relating to the abundance of *A. planci* on reefs at no time over the last 20 years has it been of sufficient detail to provide an accurate assessment of the extent of outbreaks on the Great Barrier Reef. As a consequence, great controversy has surrounded this question and it has involved both the public and the scientific community (Kenchington, 1978). Even recently little agreement has been reached among scientists as to the extent of the Great Barrier Reef affected during the second series of outbreaks since 1979 (Crown of Thorns Starfish Advisory Committee, 1985; see also Endean & Cameron, 1985). Accurate information which will enable definitive statements to be made regarding the extent of outbreaks has been difficult to obtain for the following reasons.

- (1) It is impossible to survey entirely the Great Barrier Reef since it is so large and heterogeneous a structure. Such an undertaking would

- require unlimited resources as well as personnel and time. During 1985 surveys of approximately 10% of the total number of reefs in the Great Barrier Reef were conducted (as part of an employment programme) at a cost of A\$ 1 million (Bradbury, Done *et al.*, 1985).
- (2) Outbreaks are not uniform phenomena, but vary substantially in population size and the extent of reef that they encompass (Moran, Bradbury & Reichelt, 1985). Recent studies on John Brewer Reef have demonstrated that major temporal and spatial changes in the distribution and abundance of starfish may be quite rapid occurring in the order of months rather than years (Moran, Reichelt & Bradbury, 1985).
 - (3) Estimates of the abundance of starfish and corals have been conducted using different methods making it difficult to compare and analyse the data collected.

Given the problems listed above it is clear that the degree of information required to provide an 'error-free' assessment of the extent of outbreaks on the Great Barrier Reef or any other large reefal system will never be attained. For this reason it should be recognized that debates focusing on this issue may never be fully resolved. Despite the fact that a definitive answer is not likely to be forthcoming, information may be obtained which will allow reliable predictions to be made regarding the extent of outbreaks. Information of this type can be gained by repeatedly surveying a smaller proportion of reefs situated uniformly throughout the reefal system. This will generate a homogeneous information base which will be amenable to mathematical analysis.

EFFECTS OF OUTBREAKS

EXTENT OF CORAL MORTALITY

Pearson (1981) in reviewing the information available on the recovery and recolonization of coral communities stated that outbreaks of *A. planci* caused coral mortality that was more extensive and dramatic than any other natural or man-made disturbance (Fig. 8a,b,c). Various estimates have been given of the extent of coral mortality which can be inflicted by outbreaks of starfish. Chesher (1969a) reported that outbreaks in Guam were destroying corals at an average rate of 1 km per month. On the Great Barrier Reef outbreaks were indicated to have killed approximately 80% of all corals down to a depth of 40 m at Green Island (Pearson & Endean, 1969). Higher figures of coral mortality were given for Fitzroy Island (Pearson & Endean, 1969) and recently for Green Island (Endean, 1982). These reports indicate that outbreaks of *A. planci* are capable of killing large areas of coral, but not all outbreaks produce such destruction. For example, the outbreak in Hawaii was found to have had little effect on the coral populations by the time it had dispersed (Branham *et al.*, 1971). In addition, Glynn (1973, 1974) considered that although starfish were common on reefs in Panama their level of predation was not enough to alter coral community structure as they preferred to feed on less abundant corals. These findings opposed

those of Porter (1972, 1974) who suggested that *A. planci* fed preferentially on competitively dominant species (*Pocillopora damicornis*) and thus was responsible for creating a more diverse coral assemblage composed of less preferred species. Glynn (1976) argued that the surveys undertaken by Porter were inadequate as a large proportion of them were carried out in shallow water and not in areas where most *Acanthaster planci* were found. He also showed that *Pocillopora damicornis* is not a preferred food source due to the occurrence of symbionts (*Alpheus* sp. and *Trapezia* sp.) which live in the coral and prevent the starfish from feeding (Glynn, 1976, 1980). Glynn (1976) suggested several other factors which could account for the community patterns identified by Porter (1972) and these have been summarized by Menge (1982).

The information given above suggests that outbreaks of *Acanthaster planci* may not kill all the coral in an area (Rowe & Vail, 1984b). Outbreaks themselves are variable phenomena, both spatially and temporally and the amount of coral damage on a reef is not always evenly apportioned. For example, it has been reported on numerous occasions that corals in shallow water tend to survive starfish outbreaks because of the turbulent conditions (Endean & Stablum, 1973a; Colgan, 1982; Moran, Bradbury & Reichelt, 1985). Also, certain species of corals, particularly massive forms, may be left after outbreaks because generally they are not a preferred food (e.g. *Pocillopora damicornis*, *Porites* spp., *Diploastrea* sp.) (Glynn, 1976; Endean & Stablum, 1973a; Pearson, 1974). Recently, Done (1985) suggested that the mortality of some of these corals may be a function of the size of the colony. In a series of extensive surveys on John Brewer Reef they found that massive colonies of *Porites* spp. greater than 500–600 mm were less susceptible to predation by *Acanthaster planci*. Even large massive *Porites* that had suffered predation were most often not killed entirely and the live surfaces were observed to regrow over the dead surfaces forming knob-like protrusions (Woodhead, 1971; Done, 1985). Done also demonstrated that areas which may have suffered almost 100% loss of coral cover may contain large numbers (up to 59 per m²) of small, remnant colonies (10–100 mm) that had escaped starfish predation. Thus the term “devastation” must be used with caution when describing reefs that have suffered extensive coral mortality.

Since coral mortality is not uniform on reefs and some corals survive starfish predation better than others, it becomes very difficult to determine the extent of coral damage caused by outbreaks. This is particularly true when trying to assess the amount of mortality over an entire reef surface since survey methods which may be suitable for recording coral mortality in small areas (e.g. line transects and quadrats) may not give accurate information over this much larger area. More broad-scale survey techniques (e.g. manta towing and spot checks) may be needed in order to obtain information on coral mortality at the whole reef scale (Kenchington & Morton, 1976; Pearson & Garrett, 1975, 1976, 1978). Care must, however, be taken when conducting such surveys as areas of dead white coral (termed feeding scars when caused by *Acanthaster planci*) (Fig. 8b) may also be caused by other means. A variety of different animals have been reported to feed on coral although most of them are unlikely to produce extensive areas of mortality (Endean, 1971a; Glynn, 1985). While this is generally true,

several animals are capable of causing large areas of dead white coral which may be mistaken for the recent predatory activities of *A. planci*. For example, the gastropods *Drupella fragum* and *D. rugosa* have been demonstrated to be responsible for causing extensive coral mortality (up to 35% of coral cover destroyed) in Japan and the Philippines, respectively (Moyer, Emerson & Rose, 1982). Similarly, the starfish *Culcita novae-guineae* may be a significant cause of dead white coral in certain parts of the Indo-Pacific region (Goreau *et al.*, 1972). The gastropod *Jenneria pustula* was recorded by Glynn, Stewart & McCosker (1972) to occur in large populations (up to 18 000 individuals) on reefs in Panama. At those densities it was found that this animal could destroy 5.26 metric tons of *Pocillopora damicornis* per hectare per year. This rate of destruction was estimated to be equivalent to that generated by a population of *Acanthaster planci* at a density of 30 individuals per hectare. Other animals which have been reported to produce significant amounts of coral mortality are hermit crabs, puffer fish (Glynn, 1974) and the starfish *Pharia pyramidata* (Dana & Wolfson, 1970). In addition, not all dead white coral may result from the feeding activities of animals alone. Coral bleaching which has been reported recently in Panama (Glynn, 1983, 1984a) and on the Great Barrier Reef (Harriott, 1985; Fisk & Done, 1985; Oliver, 1985) may affect up to 50–80% of coral cover on some reefs. It follows that recently dead coral on reefs may not indicate the presence of large numbers of *Acanthaster planci*, but may represent the effects of other biotic and abiotic factors. Thus care must be taken when using the abundance of feeding scars as a measure of the extent of the activities of this starfish.

Recently, Cameron & Endean (1985) have suggested that the severity of

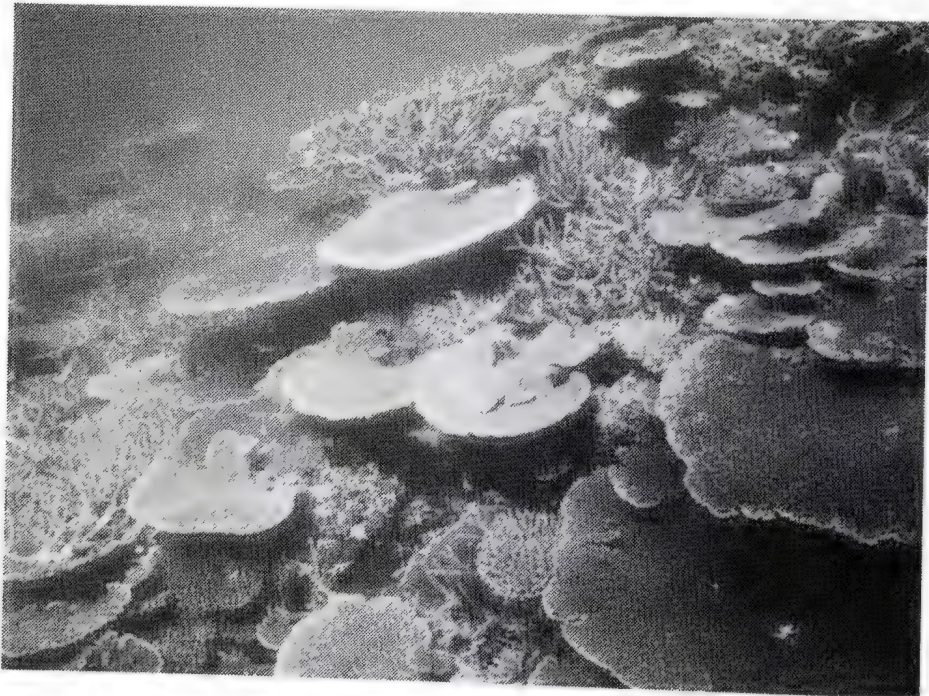


Fig. 8(a)



Fig. 8(b)

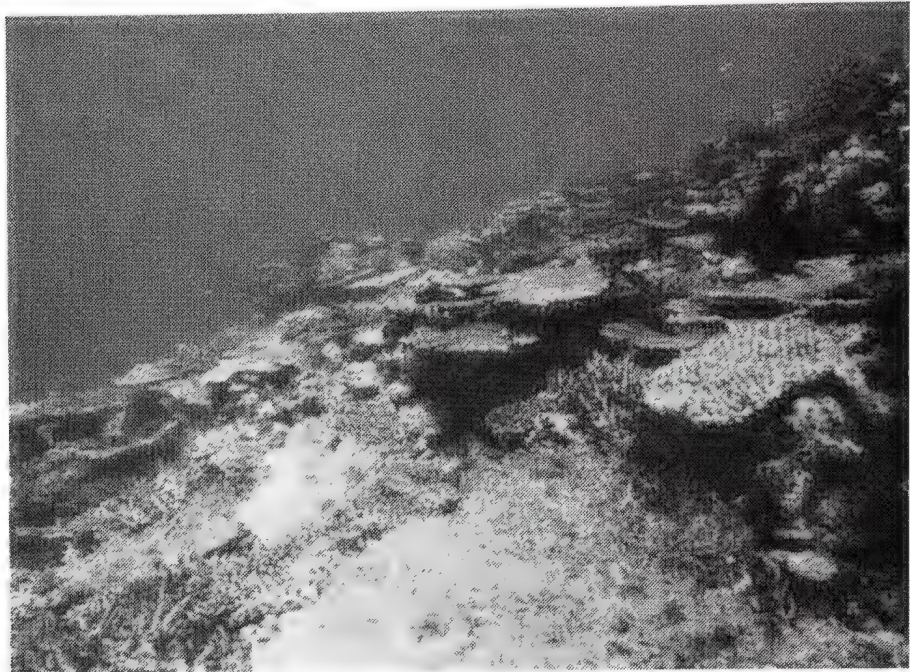


Fig. 8c

Fig. 8.—Before (a), during (b) (note patches of white coral), and after (c) an outbreak of starfish.

an outbreak should be judged not only according to how much coral mortality it produces but also on the types of coral species killed. They argued cogently that long-lived corals (e.g. *Porites* spp.), rather than transient species, were the main architects of coral community structure. Based on this argument they used the term “ecocatastrophe” to describe the second outbreak on the Great Barrier Reef as they claimed that many massive corals had been killed (Endean & Cameron, 1985). They used this emotive term since they considered that this outbreak, unlike the first, had succeeded in removing those corals which made up the very fabric of the Reef. They did not, however, present much quantitative evidence to bolster these assertions.

CORAL RECOVERY

One of the first changes which has been observed after an outbreak has occurred is the recolonization of the dead surfaces by algae. It has been commonly reported that once a coral has been killed the bare white surface is quickly colonized by these organisms (Pearson & Endean, 1969; Endean & Stablum, 1973a; Nakasone *et al.*, 1974). This led Cameron & Endean (1982) to suggest that after outbreaks the reefs are dominated initially by algae. A number of studies have investigated this process in more detail. In general, it would seem that the rate and pattern of recolonization vary according to location. In the Red Sea, Biggs & Eminson (1977) found that corals predated by *Acanthaster planci* were rapidly covered by algae which reached their maximum growth after two weeks. They suggested that

feeding scars could only be recognized in the field within ten days of the death of the coral. On the basis of these findings they advised that feeding scars may not be reliable indices of the extent of predation on reefs. Price (1972, 1975) found algal colonization of dead corals to be much slower on the Great Barrier Reef. Algae did not become apparent until almost two weeks after the death of the coral. Recording the recolonization of algae over a period of 77 weeks he reported that turf algae and blue green algae were important during the early stages of the development of the algal community. The turf algal coverage declined after about one year and encrusting algal forms then dominated the community. As these forms were thought to consolidate the corals, Price (1975) considered it unlikely that they would be eroded as suggested by Fishelson (1973). Belk & Belk (1975) studied the processes involved in the recolonization of algae on recently killed *Acropora aspera* colonies in Guam. They discovered that dead surfaces were covered by three species of blue-green algae and two species of red algae within 24 hours. Most algal species recorded during this study had settled within nine days. Two species of blue-green algae dominated the substrata within the first 25 days after which time they were dominated by the brown alga, *Giffordia indica*.

The processes involved in the recolonization and development of hard corals have been investigated in several studies. So far, however, no long term study has been conducted where coral community structure has been surveyed before and after an outbreak of starfish at the same site. Surveys of community structure prior to an outbreak may provide information which can be used to assess accurately the extent of recovery. Studies of this sort have only been recently initiated (Done, 1985; Moran, Bradbury & Reichelt, 1985).

During the series of outbreaks that occurred on the Great Barrier Reef in the 1960s and 1970s a broad series of surveys of coral recolonization were conducted by Endean & Stablum (1973a). Recovery was assessed visually as well as by photographic techniques which had been developed earlier by Laxton & Stablum (1974). Pearson (1981) has given a thorough account of this latter method and has raised certain doubts about its accuracy. Endean & Stablum (1973a) found little if any recolonization on reefs affected by outbreaks, but as Pearson (1981) pointed out it is not possible to determine how long these processes had been underway on these reefs. The major findings of the studies undertaken by Endean & Stablum (1973a) were as follows.

- (1) Recolonization was most rapid in shallow areas on seaward slopes where many corals had survived.
- (2) Recolonization in deeper water and in sheltered locations (back reefs and lagoons) was found to be slow and often dominated by soft corals and algae.
- (3) Encrusted skeletons of dead coral may remain *in situ* for several years although there was an indication that the skeletons of some colonies (e.g. *Acropora hyacinthus*) tend to collapse due perhaps to the activities of boring animals.
- (4) In the early stages of recolonization soft coral cover was noted to have increased on many reefs.

- (5) The most common recolonizing hard coral species were: *Pocillopora damicornis*, *Seriatopora hystrix*, *Stylophora pistillata*, *Acropora hyacinthus*, *A. humilis*, *A. variabilis*, *A. formosa*, *A. cuneata*, *A. echinata*, *Porites* spp., and *Turbinaria* spp.

Endean & Stablum (1973a) and Endean (1974, 1976, 1977) considered that recovery of corals from outbreaks of *Acanthaster planci* may take from 20–40 years although they indicated that it may be slow or even retarded in some areas particularly if the skeletons of dead corals were eroded. There have been several other qualitative or visual reports of the recovery and recolonization of coral communities. For example, Branham (1973) recorded substantial recolonization of corals in Hawaii which had suffered extensive damage as a result of an outbreak which had occurred only three years previously. In Japan, Nishihira & Yamazato (1974) noted that recolonization was variable in different areas being dominated not only by hard corals but also by soft corals and algae. Only two quantitative long-term studies on the recovery of coral communities have been conducted after outbreaks of starfish, one on the Great Barrier Reef (Pearson, 1972a, 1973, 1974, 1975a, 1977, 1981) and the other at Guam (Randall, 1973a,b,c,d; Colgan, 1981, 1982).

Pearson (1974, 1981) investigated the recovery of coral communities using permanent 10 m × 1 m study plots on several reefs (Feather, Ellison, and John Brewer) and 1 m × 1 m quadrats spaced evenly along transects laid down the seaward slopes of 18 reefs between Innisfail and Townsville (Fig. 7, see p. 431). In this series of studies all permanent plots and quadrats were established a few years after the outbreaks had disappeared. In order to assess the extent of recovery the results from these surveys were compared with those obtained from nearby reefs which had not been affected by the outbreaks. The results from the surveys of quadrats and permanent plots are given in Tables XI and XII, respectively. The major findings were as follows.

- (1) The pattern of recovery was variable between reefs and within specific locations on reefs (Pearson, 1981).
- (2) There is potential for the rapid recovery of reefs since recruitment (202 new colonies were found in seven months in one plot) and growth of some species was rapid (*Acropora* spp. were found to reach 200 mm in diameter three years after settlement on artificial substrata) (Pearson, 1974, 1975a).
- (3) The most common recolonizers were *Acropora* spp. and *Porites* spp. and the rapid increase in hard coral cover was due mainly to the growth of tabular colonies (some had reached 500–1000 mm in diameter in approximately ten years) (Pearson, 1975a, 1977, 1981).
- (4) Coral recovery was slower in more unfavourable environments such as reef flats than in deeper locations on seaward slopes (Pearson, 1981).
- (5) Coral cover and density (of colonies and species) reached levels similar to those on nearby undamaged reefs within 10–15 years.

In discussing the results of these surveys Pearson (1981) suggested that a number of factors may influence the type and speed of recovery including;

TABLE XI
Comparison of coral communities on reefs recovering from starfish outbreaks (in 1966–1967) with those on reefs unaffected by them: this information is from quadrat surveys conducted off Innisfail by Pearson (1974, 1981)

State	Reef		Year	Cover(%)	Hard corals		Number of transects
	Number				Species (m ⁻²)	Colonies (m ⁻²)	
Undamaged							
Recovering	7		1971	28.2	7.2	10.5	10
Recovering	10		1971	8.2	5.6	5.1	15
Recovering	1		1975	16.0	7.7	7.0	2
Recovering	10		1977	21.4	11.4	10.8	15

TABLE XII

*Information on the recovery of coral communities in permanent study areas (2–3 m depth) on three reefs in the Great Barrier Reef: this information is taken from Pearson (1981); *from Done, 1985*

Reef	Year	Coral cover (%)	Colony size (cm) (\bar{x})	Common recolonizers	
				Genus	(% proportion)
Feather	1972	12.3	5.1	<i>Acropora</i>	(39.6)
				<i>Porites</i>	(22.3)
				<i>Galaxea</i>	(10.9)
Feather	1974	63.0	—	—	—
Feather	1975	60.0	7.3	<i>Acropora</i>	(43.7)
				<i>Galaxea</i>	(7.2)
				<i>Porites</i>	(6.7)
				<i>Pocillopora</i>	(5.5)
				<i>Acropora</i>	(59.0)
Ellison	1972	2.6	4.4	<i>Favia complex</i>	(10.0)
				<i>Porites</i>	(9.3)
				—	—
Ellison	1975	60.0	11.6	—	—
Ellison	1978	80.6	—	<i>Acropora</i>	(71.2)
				<i>Seriatopora</i>	(5.1)
				<i>Porites</i>	(5.1)
John Brewer	1974	6.0	3.6	—	—
John Brewer	1978	45.2	6.9	<i>Acropora</i>	(30.0)
				<i>Favia complex</i>	(6.7)
				<i>Fungia</i>	(4.7)
	1982*	78.0	—	—	—

type of substratum (whether or not it is algal-covered), sedimentation, growth rates of species, predation, further disturbances, environmental variables (e.g. light intensity, water circulation), location, recruitment, and settlement. He also stated that there was no evidence to support the notion that soft corals overgrew areas of hard corals killed by *Acanthaster planci*.

The studies instigated by Randall (1973a,b,c,d) at Guam were not all undertaken at the same locations. Coral recovery was followed in a number of reef zones at Tanguisson Bay from 1970 to 1974. The recovering communities were compared with those at Tumon Bay (about 10 km south) that had been surveyed prior to the outbreaks (during 1968). Unfortunately, at this site systematic surveys were not undertaken in the submarine terrace (6–18 m) or seaward slope (18–35 m) zones where coral mortality was greatest. This study was recently extended by Colgan (1981, 1982) who reported on the recovery of the coral communities up to 1980 in these two zones, as well as the reef front zone (0–6 m). The data obtained from all these studies are given in Table XIII. It is difficult to compare them directly as three different survey methods (line transect, quadrats, point-quarter) were utilized during the period of the entire study. Despite this Colgan (1982) identified five stages in the recovery of the communities at Tanguisson Bay.

- (1) Dominance of crustose and filamentous algae.
- (2) Recruitment of planulae.
- (3) Differentiation of growth forms (from encrusting to massive and corymbose).

TABLE XIII
Information on coral communities obtained before (during 1968 at Tumon Bay) and after (from 1970–1981 at Tanguisson Bay) an outbreak of starfish, for three reef zones at Guam: these data were taken from Randall (1973a,b,c,d) and Colgan (1981, 1982); *total number of species recorded over all reef zones for each year

	Reef front					Submarine terrace					Seaward slope				
	1968	1970	1971	1974	1981	1968	1970	1971	1974	1981	1968	1970	1971	1974	1981
Coral cover (%)	49.0	20.9	21.9	24.8	43.7	59.1	0.9	4.0	12.0	65.9	50.1	0.5	2.1	6.3	36.2
No. colonies (m ⁻²)	—	16.7	20.8	24.2	24.7	—	8.0	15.8	24.7	31.1	—	4.0	13.1	21.5	43.8
No. species (m ⁻²)	—	5.4	6.7	7.5	7.5	—	4.8	6.4	8.0	10.8	—	2.1	6.0	8.0	13.1
Species richness	98 (139)	70 (91)	68 (105)	— (131)	— (137)*	73	47	70	—	—	57	32	61	—	—
Growth form (%) frequency)															
Massive	25.4	20.3	15.5	32.4	33.3	—	12.8	7.0	32.1	22.6	—	8.8	10.8	46.4	36.9
Encrusting	24.4	59.5	62.2	26.4	25.8	—	78.1	84.3	58.2	61.0	—	80.8	80.0	39.1	41.0
Branching	43.6	8.5	21.4	39.2	38.3	—	1.6	5.2	8.8	15.0	—	5.0	4.6	9.9	14.8
Other	6.6	11.7	0.9	2.0	2.6	—	7.5	3.5	0.9	1.4	—	5.4	4.6	4.6	7.3

- (4) Expansion of colonies (this lead to a reduction in the number of coral colonies).
- (5) Competition between corals.

Like Pearson (1981), Colgan (1982) found that coral cover had regenerated to levels recorded before the outbreak in about 11 years. He also noted that the species richness and size frequency distribution of the communities had recovered in this time. Initially, recovery in the areas at Tanguisson Bay was slow until adults became re-established and this was thought to occur as a result of regrowth from small remnants and recruitment from nearby surviving adults. It was evident that numerous small colonies survived, since after the outbreak the zones were found to have relatively high species diversity and species richness although coral cover was only 1%. In 1970 (about two years after the outbreak), 87% of the corals at Tanguisson Bay were less than 100 mm (Randall, 1973b). As noted earlier, Done (1985) reported high densities of small remnants (10–100 mm) in areas of John Brewer Reef just after they had experienced extensive starfish outbreaks. Colgan (1981) considered that these survivors enabled rapid recovery of the coral communities at the local scale.

The studies of Pearson and Colgan have demonstrated that some of the variables which characterize coral communities may return to their original levels within 10–15 years. Despite this they have not shown whether the structure of these communities may recover in such a period. Colgan (1981) stated that the species diversity of the communities at Tanguisson Bay (gauged using diversity indices) had “approached or exceeded” the values recorded at Tumon Bay prior to the outbreak, although no values were given for this latter area. Pearson (1981) felt that it may take several decades for coral communities to recover completely. More long-term, before and after studies are needed in order to resolve this question.

OTHER COMMUNITIES

The severity of starfish outbreaks has been gauged most often according to the extent of their effects on the hard coral communities which are a major component of the physical structure of reefs. Perturbations of this scale are likely to influence the distribution and abundance of other organisms which may interact with or depend on this complex assemblage of corals. Few studies have been conducted to ascertain whether the creation of large areas of dead coral has ‘downstream’ effects on other communities. References to such effects have mainly come from incidental field observations and have not resulted from quantitative studies. For example, Laxton (1974) suggested that the distribution of the blue starfish *Linckia* sp. had been extended on some reefs as outbreaks had caused an increase in the cover of coralline algae. Similarly, Garlovsky & Bergquist (1970) noted that the annelid *Palola siciliensis* had declined in abundance in Western Samoa in conjunction with the increase in numbers of *Acanthaster planci*. In this instance outbreaks were thought to have caused the destruction of much of the habitat of this animal. Outbreaks have also been thought to lead to the dominance of soft corals on certain reefs (Endean, 1971a), presumably because they are generally not eaten by starfish and have the opportunity to

grow into those areas of coral destroyed by *A. planci*. While Garrett (1975) found that some soft corals are competitively dominant over smaller hard corals, evidence from studies of coral recovery have indicated that they are not a particularly important component of this process (Pearson, 1981).

Most references to 'downstream' effects on other communities have been in relation to fish communities. Observations by Chesher (1969a), Cheney (1972c), and Endean & Stablum (1973b) indicated that algal feeding fish such as acanthurids and scarids were more common after outbreaks but that chaetodontids and serranids gradually disappeared sometime after these events. In general, these conclusions have been supported by the results of two studies which have investigated the effects of outbreaks on coral reef fish communities. The first by Sano, Shimizu & Nose (1984) involved manipulative experiments on a small number of coral colonies. The results from these experiments were then compared with observations of fish communities near corals that had been killed by *A. planci*. From these studies they predicted that coral feeding species (e.g. chaetodontids and serranids) may decrease significantly in abundance after outbreaks. They postulated that this was due to the lack of available food. They also predicted a decrease in the species richness of resident fish that used the corals as a habitat (e.g. pomacentrids and apogonids) and a decline in the overall diversity of fish species. Not all results in this study were clear cut. For example, they found that the quantitative increase in algal cover had little or no effect on the species richness and abundance of herbivorous and omnivorous fish. The study by Sano *et al.* (1984) utilized information on the change of fish communities in single coral colonies to predict the likely changes which may occur over large areas of reef. This procedure assumes that interactions at the coral colony level will also be manifested at the coral community level.

Studies by Williams (1986) attempted to determine whether fish communities were affected over large areas by extensive outbreaks of *A. planci*. During these studies detailed visual surveys of fish were undertaken at several locations on reefs before and after outbreaks of starfish. The outbreaks were found to have caused a significant reduction in the abundance of chaetodontids. This was the only major change that could be readily attributed to the effects of the outbreaks. Williams suggested that they may have more long term effects by indirectly altering the growth rates and fecundity of fish, as well as making them more susceptible to predation. Changes in the type of substratum by outbreaks were thought possibly to lead to variation in the recruitment of fish. Further studies of these fish communities may indicate whether these expected long term changes in fish community structure will eventuate.

CONTROL OF *A. PLANCI*

Since the first outbreaks of *A. planci* were recorded during the late 1950s a number of control programmes have been conducted in various parts of the Indo-Pacific region. In general, control programmes were conducted in a bid to protect coral communities from widespread destruction although some (e.g. the programme undertaken at Nauru) were carried out for little

apparent reason and yielded few starfish. A list of these programmes is given in Table XIV.

It is clear from the scientific literature that an enormous number of starfish (approximately 14.6 million) have been killed or removed from reefs throughout the Indo-Pacific since the late 1950s. Relatively few control programmes have been undertaken on the Great Barrier Reef despite it being the largest reef system in the world and they have been mainly centred in areas used for tourism (e.g. Green Island, John Brewer Reef). By far the largest control programme has been that undertaken in the Ryukyu Islands. Yamaguchi (1985, in press) recently stated that almost 13 million starfish were removed from the reefs in this area over the period from 1970 to 1983 at an estimated cost of 600 million yen (almost \$A 2.6 million). Other large control programmes have been conducted in Micronesia and Samoa (Table XIV).

A variety of different techniques were employed in these programmes to reduce starfish numbers. Initially at Green Island starfish were killed by chopping them up. This was abandoned as at the time it was thought that the starfish could regenerate from its severed parts (Gouldthorpe, 1968). Although other species of starfish are capable of doing this there is little evidence to suggest that *A. planci* has this ability. Owens (1971) cut a specimen of *A. planci* in half and found that within one week the two halves had rejoined. By re-separating them he was able to generate two new individuals which appeared after one month to be healthy and capable of feeding. An additional experiment by Owens (1971) failed to reproduce this result. Similar tests by Pearson & Endean (1969) also resulted in the death of starfish. For fear of increasing the population, later control programmes at Green Island involved collecting starfish and burying them on land. This method has been used in the majority of programmes conducted throughout the Indo-Pacific. Many of those killed in Micronesia and the Ryukyu Islands were destroyed in this fashion (Cheney, 1973; Yamaguchi, in press).

Collection by hand is both time consuming and labour intensive (Endean, 1969) and consequently several other methods have been tested as a means of efficiently reducing starfish numbers. Most involve the injection of various substances such as: 100% formalin, 10% acetic acid and 90% formalin (Owens, 1971), 18% ammonium hydroxide (Nishihira & Yamazato, 1972) and household ammonia (Branham *et al.*, 1971). While each method was found to be time efficient not all of the starfish injected were killed. Kenchington & Pearson (1982) reported the results of a test comparing three methods of control; collection by hand, collection with compressed air, and injection with copper sulphate. Killing starfish by copper sulphate injection was found to be the most efficient (132 starfish killed per hour per diver) of the three methods tested. Apart from these methods, Endean (1969) has reported that application of quicklime to the surfaces of starfish may be a useful way of controlling starfish numbers. This method, which was found to kill *A. planci* within approximately 24–48 hours, has been used to control outbreaks of *Asterias forbesi* in the United States (Loosanoff & Engle, 1938, 1942).

All of the above methods involve controlling starfish numbers at the level of the individual. During the 1960s and early 1970s an attempt was made to develop a mass control method which could be used to exclude starfish from

TABLE XIV
Acanthaster planci control programmes in the Indo-Pacific region: *denotes total for region

Region	Year	Number reported killed	References
Cook Islands	1973	80 974	Birkeland, 1982
Fiji	1970	9 860	Owens, 1971
Great Barrier Reef		93 312*	
Green Island	1966-1968	44 000	Barnes, 1966, Harding, 1968
John Brewer Reef	1980	25 850	Kenchington & Pearson, 1982
Beaver Reef	1983-1984	3 000	Tarca, pers. comm.
Beaver Reef	1966-1968	11 000	<i>Sunday Sun</i> 16 Oct. 1983
Comorant Pass	1983-1984	9 000	<i>Sunday Sun</i> 16 Oct. 1983
Hawaii	1984	462	GBRMPA, unpubl. data
Molokai		20 000*	
Molokai	1970	10 000	Branham, 1971
Japan	1972	10 000	Branham, 1973
Ashizuri-Uwakai		13 220 000*	
Kushimoto	1973-1983	87 000	Yamaguchi, in press
Miyake Island	1973-1979	1 400	Yamaguchi, in press
Ryukyu Islands	1980	3 500	Crown of Thorns Starfish Advisory Committee, 1985
	1957	220 000	Yamazato, 1969
	1970-1983	12 908 100	Yamaguchi, in press
Malaya	1971	350	Endean & Chesher, 1973
Micronesia		658 830*	
Mariana Islands	1968-1972	77 000	Tsuda, 1971, 1972; Cheney, 1972b, 1973b; Ikehara, 1972
Caroline Islands	1969-1972	226 750	Tsuda, 1971, 1972; Aisek, 1972; Marsh, 1972a, b; Nakamura, 1972; Wass, 1972; Cheney, 1973b
Marshall Islands	1977	354 470	Birkeland, 1982
Nauru	1971-1972	610	Sablan, 1972
Philippines	1971	150	Endean & Chesher, 1973
Samoa:	1974-1976	1 000	Alcala, 1976
Western American	1969-1970	13 847	Garlovsky & Bergquist, 1970
Solomon Islands	1977-1978	486 933	Birkeland & Randall, 1979
Tahiti	1971	1 000	Randall, 1972
Wake Island	1971	10 000	Devaney & Randall, 1973
	1969	300	Randall, 1972

large areas of reef. The system consisted of perforated nylex tubing which contained copper sulphate gel (Walsh *et al.*, 1971). Once submerged the copper sulphate was slowly released through the holes in the nylex tubing. This method was tested on the Great Barrier Reef but was found to be unsuccessful (Walsh *et al.*, 1976).

While a variety of toxic substances has been used to kill large numbers of *Acanthaster planci* no studies have been conducted to determine whether other reef organisms would be affected by these methods if they were undertaken on a large scale. It is possible that substances such as copper sulphate and formalin, which are known to be highly toxic to marine organisms may leach into the water after the starfish has decomposed. In addition, predators may be affected should they feed on starfish that have been injected with these substances.

During the course of outbreaks several other control methods have been suggested which include the use of electric barriers, electric guns, and suction dredging (Vine, 1970). As an alternative to employing methods which rely on direct control by man, Endean (1969) proposed that outbreaks of *A. planci* may be biologically controlled using a known predator, the giant triton shell, *Charonia tritonis*. There are several reasons why this method should be avoided. First, experience in other ecosystems has shown that methods involving biological control frequently fail, often producing many additional problems (Krebs, 1978). Secondly, very little is known about the population dynamics of the target species. This information is needed in order to implement an effective biological control programme (Krebs, 1978). Thirdly, information from several studies suggests that *C. tritonis* is not the sole predator of *Acanthaster planci* (see Table VI, p. 415) nor is *A. planci* the only prey of *Charonia tritonis*. In reality there are practically no quantitative data concerning the interaction between *C. tritonis* and its prey. Fourthly, it is not known what long-term effects this method would have on *Acanthaster planci* or the reefal communities with which it interacts. Finally, as *Charonia tritonis* is generally present in low densities on reefs (Endean, 1974) there may be an insufficient number of predators available for use as biological controls.

With the onset of outbreaks and the extensive death of corals there was considerable debate as to whether control programmes should be implemented to limit the numbers of starfish on reefs. Chesher (1970) argued that outbreaks of *Acanthaster planci* were not normal and that they may cause the permanent destruction of reefs if allowed to continue. As a result of this 'everything to gain, nothing to lose' approach Chesher proposed that control methods be implemented to limit starfish numbers. This view was also supported by Endean (1971a) and O'Gower, Bennett & McMichael (1972) who suggested that control measures will have done little harm even if outbreaks subsequently were shown to be a natural phenomenon. Newman (1970) opposed these views contending that outbreaks were probably natural events and that *A. planci* was an integral part of the ecology of reefs. He emphasized that there was insufficient evidence to indicate that coral reefs would be permanently destroyed if control methods were not implemented. On the basis of this 'everything to lose, nothing to gain' approach he advocated that it would be unwise to undertake such drastic measures.

Despite views to the contrary, control programmes were initiated throughout the Indo-Pacific. As many of these programmes were conducted at a time (late 1960s–early 1970s) when starfish populations were generally declining throughout this region it is difficult to determine whether they were successful. In general, the control programmes conducted in Micronesia were considered successful although they did not eradicate all starfish from the reefs in this region. Cheney (1973b) considered that they had caused a marked decline in starfish numbers thereby “reducing the potential for the destruction of coral cover” (p. 179). Both Tsuda (1971) and Wass (1973) also felt that these programmes had been successful although the latter author stated that the starfish populations had declined only in those areas where control measures had been introduced. It would appear that they had little effect outside these areas. Marsh & Tsuda (1973) were more cautious in evaluating the success of the control programmes in Micronesia. They were reluctant to attribute the population decline entirely to the implementation of control programmes as the starfish population on one island (Aguijan) declined substantially even though control methods were not undertaken.

Control programmes conducted in other parts of the Indo-Pacific appear to have been less successful than those in Micronesia. For example, programmes undertaken in Hawaii were only partly successful in attempting to eradicate three large aggregations of starfish. While one of the populations was eradicated another survived for a year despite being reduced to half its original size (Branham, 1973). In Australia, attempts to protect a small coral viewing area at Green Island were unsuccessful even though a diver was permanently stationed in this area to collect starfish. During the course of two years 44 000 starfish were removed from the area. Unfortunately, these intensive control measures were unable to prevent the starfish from causing considerable damage to the coral communities in this area (Barnes, 1966; Harding, 1968). Flanigan & Lamberts (1981) reported that control measures did not significantly alter the starfish populations in American Samoa despite the fact that almost 500 000 individuals were killed in this region.

It must be seriously questioned whether control programmes are of value in limiting starfish numbers and preventing widespread coral mortality given the results of programmes conducted in the Ryukyu Islands. Yamaguchi (1985, *in press*) concluded that they had been largely ineffective in preventing the destruction of considerable areas of reef even though an enormous number of starfish were killed. He stated that there were two main reasons why these costly programmes had failed to achieve their objectives. First, for fiscal reasons they were slow in commencing which meant that some outbreaks had been established on reefs for up to a year before control measures were implemented. This lag ensured that the outbreaks often were left undisturbed for at least one spawning period allowing them the opportunity to propagate and thus increase their size and distribution. Secondly, as control measures were conducted on the basis of collecting efficiency relatively large numbers of starfish were left after the programmes had finished. Outbreaks have occurred on many reefs in the Ryukyu Islands over the last 15 years. The persistence of these populations is thought to have caused a wave of outbreaks at Ashizuri-Uwakai,

Kushimoto (Japan) and at Miyake Island (Yamaguchi, in press) (see Fig. 6). Control measures were also implemented at these three locations. The control programme at Miyake Island was the only one considered to have been successful in eradicating the starfish (Yamaguchi, in press).

These results aside, the usefulness of control programmes must be further doubted with the re-occurrence of outbreaks of *A. planci* in areas where control measures had been undertaken up to a decade before. Examples of such areas are Green Island (Kenchington & Pearson, 1982), Guam and Palau (Birkeland, 1982). In hindsight it would seem that control programmes may represent only a short-term solution to the problem of widespread outbreaks of *A. planci* in the Indo-Pacific region. While control measures may change the local abundance of *A. planci* on a reef they may have little, if any effect on the occurrence of outbreaks in the future. This conclusion was reached by Bradbury *et al.* (1985a) who constructed a qualitative model of outbreaks based on data from the Great Barrier Reef. Using this model they provided evidence that outbreaks in this reefal system displayed a stable cyclicity whose trajectory was unlikely to be altered by attempts to change the abundance of *A. planci*.

With these conclusions in mind reef managers are faced with three possible choices. The first is to continue conducting extensive control programmes in the hope that they are in some way helping to eradicate *A. planci* and so saving our reefs from imminent destruction. While this perhaps could be likened to someone trying to hold back the tide it is none the less alluring, particularly if the outbreaks are widespread and are causing considerable coral mortality. Of course, the effects of outbreaks may be magnified if they occur in conjunction with man-related activities such as dredging, blasting, fishing, and pollution (Fagoonee, 1985a,b; De Silva, 1985; Muzik, 1985). The combination of these processes may lead to gross economic, management, and conservational problems which in turn may generate tremendous pressure to eradicate *A. planci*. The second option is to concentrate control efforts on a much smaller scale in areas which have some importance (*e.g.* tourist areas). Besides being relatively less expensive these types of control programmes may be more successful in the long-term, in protecting small areas of coral than those programmes undertaken on a much larger scale. Results so far suggest that control programmes carried out in small isolated areas (hundreds of kilometres away from other populations) have the greatest likelihood of success (*e.g.* Miyake Island). The third and final option is to do nothing. As control programmes of any sort are becoming increasingly more expensive and thus harder to justify this approach also has much to recommend it.

In the final analysis, the option chosen must depend on a host of variables which will differ according to the situation. These variables relate to the following.

- (1) Size and areal extent of the population to be contained (*e.g.* is the population too large or widespread to enable control methods to be effective?)
- (2) Position of the population (*i.e.* is it located in a remote area or an area which is easily accessible?)

- (3) Importance of the area affected (*i.e.* what is the use of the area—is the area used for tourism or some other commercial venture?)
- (4) Distance of the population from other reproductively active populations (*i.e.* is there the likelihood that recruitment may occur after the control methods have been conducted?)
- (5) Funds available (*i.e.* are sufficient funds available to complete the programme?)
- (6) Time at which funds become available (*i.e.* is the time at which funds become available the most appropriate time for initiating an effective control programme?)

The effectiveness of a control programme will depend on each of these factors being addressed in the correct manner. It may depend as much on the time when funds become available as the numbers of starfish involved in the outbreak. Recent studies on the Great Barrier Reef have demonstrated that the distribution and abundance of starfish may change quite rapidly on reefs proceeding from high densities to relatively low population levels within the space of six months (Moran, Bradbury & Reichelt, 1985). Lags in funding may cause a control programme to be ineffective by ensuring that it was implemented after the outbreak had reached its zenith. It becomes apparent, therefore, that the timing of control programmes (relative to the state of the outbreak) has a major bearing on their success.

Bearing in mind that outbreaks may move over reefs with great speed then the success of a programme will also depend on the proportion of starfish in an outbreak which are killed. Yamaguchi (in press) attributed the ineffectiveness of the control programme in the Ryukyu Islands to be partly due to the fact that only starfish which could be collected quickly (*e.g.* those in shallow waters) were killed, leaving behind a large number of individuals. By the same token removing every starfish from a particular area and disregarding those in surrounding territories may have little success. This was found at Green Island. In some areas an 'all or nothing' response may need to be considered if a control programme is going to be successful.

On a cost-benefit basis it would appear that the undertaking of concentrated control programmes in discrete locations offers the best opportunity for success using the methods presently available. The general pessimism regarding control programmes has, however, reached the stage that even this alternative is considered doubtful by some (Kenchington & Pearson, 1982). Apart from the results of the programmes at Green Island it is not clear whether such a plan can be used as a general purpose control by reef managers. It is, however, clear that it is time to re-assess the rationale governing the use of control measures and to undertake quantitative studies with the aim of developing a coherent and effective management policy in relation to the control of outbreaks of *A. planci*.

UNANSWERED QUESTIONS

While a great deal of information has been presented about various facets of the *Acanthaster* phenomenon there is still much that is not known. From that presented so far it is clear that the amount of information available on

each facet is very different and some are more well-defined than others. For example, much more is known about the biology of *A. planci* than its ecology and population dynamics. Often this lack of information arises because of experimental difficulties (e.g. evaluating the dispersal of larvae).

It can be argued from an inspection of the scientific literature and various media reports that the intense debate and controversy surrounding the *Acanthaster* phenomenon have been exacerbated because many views and hypotheses have arisen from an ignorance of what is known as well as what is not known about the subject. Previous sections in this paper have defined what is known about the phenomenon. It is also equally important to define what is not known about this subject for several reasons. First, it earmarks those facets of the subject which are most poorly understood and hence need to be intensively studied. Secondly, it stimulates the development of research questions and the subsequent delineation of research priorities. Finally, it provides a sound basis for the formulation and refutation of new theories and hypotheses.

The aim of this section is to present, in question form, those facets which are most important in understanding the phenomenon and about which there is little if any information. The following questions, which are divided into three groups (1) larvae and juveniles; (2) adults; and (3) effects on communities and processes—remain unanswered. Comprehensive information on each will provide an understanding of the following.

- (1) Why outbreaks occur and whether they are natural or unnatural phenomena.
- (2) Whether they play an important part in reefal processes and the development of reef structure.
- (3) Why some reefs are more susceptible to outbreaks than others.
- (4) Why some outbreaks cause extensive coral mortality while others do not.
- (5) How outbreaks are propagated over large distances.
- (6) Whether special management policies need to be formulated in order to prepare for the occurrence of future outbreaks.

LARVAE AND JUVENILES

- (1) Are high nutrient conditions needed for the enhanced survival of larvae in the field?
- (2) Do these types of conditions occur frequently in the field? If so, do they coincide with observed spawning periods and how long do they occur?
- (3) Can larvae develop and settle under 'non-bloom' nutrient conditions in the field. If so, can high densities of larvae be sustained under these conditions?
- (4) How important is diet in influencing the survival of larvae? Is survival more dependent on the diversity rather than density of food species? What other factors influence the survival of larvae?
- (5) Do certain physical conditions occur in the field that cause the increased survival of larvae? Do these conditions act in conjunction with any other factors?

- (6) How long do larvae spend in the plankton before settling? What is the maximum period of time they can spend in this phase and yet still be able to settle?
- (7) How far can larvae be dispersed in the field?
- (8) What factors are important in causing their dispersal?
- (9) Is there a positive correlation between larval density, recruitment density, and adult density?
- (10) Where do larvae occur in the water column? Does their position vary throughout their planktonic period? What factors are responsible for determining their position?
- (11) Where do larvae settle in the field? Is it in shallow or deep water on reefs? Do they settle in high densities?
- (12) Do larvae tend to settle on a particular type of surface? What factors are important in determining the type of surface chosen by larvae for settlement?
- (13) Are there particular areas on reefs which are more suitable for settlement than others?
- (14) Do larvae tend to settle on those reefs from which they were propagated or do they generally recruit to reefs other than the parent reef?
- (15) Do juveniles tend to be in shallow or deep water on reefs? Does this location vary depending on whether or not the reef has recently suffered an outbreak of adults?
- (16) What are the mortality rates of larvae and juveniles in the field?
- (17) Is predation important in determining the density of larvae and juveniles? What are the main predators of each stage?
- (18) Apart from predation what other factors are important in causing the mortality of juveniles (*e.g.* disease, lack of nutrients)?
- (19) What type of food do juveniles eat in the field?
- (20) How fast do juveniles grow in the field? Is it similar to that recorded in the laboratory? How important is diet in determining the growth rate of juveniles?
- (21) How far do juveniles move in the field? Do they show any feeding preferences?

ADULTS

- (1) Are adults capable of moving between reefs?
- (2) How rapidly do they grow in the field? Is their rate of growth similar to that recorded in the laboratory?
- (3) Can the age of a starfish be determined from its size?
- (4) How long do adults survive in the field?
- (5) What are the rates of mortality for adults in the field?
- (6) What is the rate of predation on adults on reefs? What are the main predators of adult starfish? Are these predators sufficient to limit adult population levels? Do the densities of these predators fluctuate markedly through time?
- (7) Are there any other factors which are important in causing the mortality of adult starfish (*e.g.* disease)?

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- (8) Do adult starfish enter a senile phase in the field where their growth declines greatly and they become infertile?
- (9) What causes the rapid disappearance of adult starfish which has been observed in the field? Is it related to density dependent factors (e.g. crowding causing loss of condition)? What happens to the majority of starfish? Do they die (e.g. from disease) or do they move to another reef?
- (10) Do the skeletal components of starfish accumulate in the sediments after times of outbreaks? Do more spines tend to accumulate during outbreaks than during times when starfish densities are low?
- (11) Do adults show a distinct preference for certain types of coral?

EFFECTS ON COMMUNITIES AND PROCESSES

- (1) Do coral communities recover from outbreaks of starfish? How long does this take? Is the pattern of recovery similar for most types of reefs and for different scales of disturbance?
- (2) What effect do outbreaks have on other communities (e.g. fish, soft corals)? Is this effect permanent or do these communities recover from such a disturbance?
- (3) What effect do outbreaks have on reef processes such as calcification, primary production, and reef growth?

REASONS FOR OUTBREAKS

HYPOTHESES

A number of hypotheses have been formulated to account for the occurrence of outbreaks in the Indo-Pacific region over the last 25 years. The hypotheses that have been developed fall into one of two categories; those based on the premise that outbreaks of *A. planci* are natural phenomena and those that assume them to be unnatural. Hypotheses which emphasize that outbreaks are natural phenomena are based on the view that the variability observed in the population structure of *A. planci* over both temporal and spatial scales is normal (Dana, 1970; Newman, 1970; Vine, 1970). Such a view assumes that the wide population fluctuations of *A. planci* are representative of the normal variability which can occur within animal populations on coral reefs. Moore (1978) has argued from a theoretical approach that large population fluctuations of *A. planci* can occur naturally without man's intervention. He considered that the life history characteristics of *A. planci* were indicative of a binomic behaviour which conformed broadly to the exploitation of habitats. Since organisms with this type of ability (denoted *r*-strategists) exhibit large scale population fluctuations Moore (1978) regarded outbreaks of *A. planci* to be normal and "inherent of this mode of living" (p. 57). These conclusions must be questioned as they were based on limited information. Although very little is known about the movement of starfish Moore surmised that migration was an important factor in the rate of mortality of starfish. Similarly, he assumed that *A. planci* reproduced repeatedly throughout its life cycle

although this may not be true in the light of results presented by Lucas (1984) who showed that adults may enter a senile phase.

Besides arguing from a theoretical perspective, attempts have been made to verify the belief that outbreaks are natural by demonstrating that they have occurred in the past. From information of this sort it is inferred that the present starfish outbreaks are periodic or cyclic phenomena which are natural in origin. Several authors have used historical records to show that outbreaks have occurred previously (Dana, 1970; Newman, 1970). Vine (1973) suggested that *A. planci* was abundant and had a wide distribution in much earlier times. As the records he used did not give accurate data on starfish numbers and were largely anecdotal it is, however, difficult to assess the value of this information. This criticism has been levelled at all studies which have adopted this approach (Endean, 1973b). In fact, several authors have insisted that there is no historical evidence to indicate that outbreaks of *A. planci* have taken place prior to the 1950s (Chesher, 1969a; Randall, 1972; Endean, 1977, 1982; Cameron & Endean, 1982). Also, Branham (1973) stated that anecdotal references to large concentrations of starfish may in fact refer to normal aggregations of individuals during spawning.

In addition to the above argument it has been proposed that outbreaks occurred in the past but that they went largely unnoticed and it only has been with the advent of SCUBA equipment and the increased use of coral reef environments (for tourism and research) that they have been recorded recently (Newman, 1970; Weber & Woodhead, 1970). It is no doubt true that these factors have been responsible for our greater awareness of the distribution and abundance of *A. planci*; it is, however, sheer speculation to suggest anything more than this. Randall (1972) considered that it would be unlikely for such dramatic events to be overlooked, particularly in areas which were close to human settlements and which had been used over many years for diving and fishing.

Birkeland & Randall (1979) provided evidence, after interviewing a number of old fishermen, that outbreaks of *A. planci* may have occurred at the beginning of this century in Samoa. In some instances the information they collected was, however, conflicting. Some Samoan fisherman reported that *A. planci* (termed "Alamea") had been abundant in 1916 but had been scarce since then, while others suggested that large numbers of this starfish also had been present during 1932. Again, as no records of the numbers of starfish were given it is difficult to ascertain whether they refer to normal populations of *A. planci* or outbreaking populations.

Flanigan & Lamberts (1981) proposed that *A. planci* had been well known in Samoa for many years as information on this animal could be found in records of the verbal history, linguistics, and proverbs of this country's culture. Birkeland (1981) used a similar approach to show that outbreaks were a natural and recurring phenomenon in Micronesia. He maintained that this could be implied since several high cultures in this region were familiar with this starfish, each having their own particular name for this species and advice on how to cure its sting (by applying the stomach of the starfish to the wound). Birkeland (1981) suggested that *A. planci* must have been present perhaps abundantly, for many years for this type of information to have been incorporated into these cultures.

It is not surprising that *A. planci* has been known to these cultures for

many years as the earliest records of this starfish date back to 1705 when it was first described by Rumphius. The occurrence of past outbreaks in Micronesia and Samoa cannot, however, be inferred from the information given by Flanigan & Lamberts (1981) and Birkeland (1981) as the importance of *A. planci* in these cultures may result from other factors (e.g. its appearance, toxic nature) rather than a recognition of its having occurred in large numbers at some stage in the past.

There have been very few studies that have tried to provide direct evidence of the occurrence of outbreaks in the past. During the early 1970s Maxwell (1971) reported finding skeletal debris in sediment samples from various reefs in the Great Barrier Reef, which suggested that there had been an increase in the number of echinoderms about 300, 800, and 1500 years ago. He also found that the percentage of echinoderm fragments in sediment samples increased from south to north along the Reef. As the remains of *A. planci* could not be differentiated from those of other echinoderms these results were considered to have little relevance to the debate concerning previous outbreaks of *A. planci* (Endean, 1971b; Talbot, 1971). A more extensive geological study was undertaken on the Great Barrier Reef a few years later by Frankel (1975a,b, 1977, 1978). In this study he sought to demonstrate, by searching for the presence of skeletal remains of *A. planci* in surface and sub-surface sediments, that outbreaks were a recurring phenomenon. He obtained 54 sub-surface samples from 27 reefs between Lizard Island and Gould Reef and found skeletal remains of *A. planci* in horizons from 16 of these reefs. The age of these remains were determined by dating the sediment surrounding them. From this work Frankel concluded that outbreaks of *A. planci* had occurred up to 3355 years B.P. and that they were "natural phenomena".

The conclusions of Frankel have been both accepted and criticized. Endean (1977, 1982) stated that the studies conducted by Frankel did not provide evidence of previous aggregations for three main reasons. First, *A. planci* has probably been a component of reefal ecosystems for a number of years and it is natural that skeletal remains from this animal would be deposited in the sediments. Secondly, no mass mortalities of starfish have been recorded on reefs; this is important as it is presumed that more skeletal fragments accumulate in sediments during outbreaks as a result of the mass mortality of starfish. Finally, Endean (1977, 1982) argued that it was difficult to determine the significance of skeletal debris since it was not known how many skeletal fragments were needed in a sediment horizon to constitute a past outbreak.

With the occurrence of another, recent series of outbreaks in various parts of the Indo-Pacific (Birkeland, 1982; Endean, 1982) the debate concerning the occurrence of past outbreaks has re-emerged. Several authors have considered that the data presented by Frankel (1977, 1978) provide direct evidence that large aggregations of *A. planci* occurred in the geological past (Bennett, 1981; Potts, 1981; Birkeland, 1982; Rowe & Vail, 1984b). Recently, this data was statistically re-evaluated by Moran, Reichelt & Bradbury (1986). Using the results from starfish surveys (Fig. 7) they were able to establish whether reefs had experienced a recent outbreak prior to being sampled. This information was combined with Frankel's own results for reefs where recent skeletal material was found. The combined data were

arrayed in a contingency table and analysed using a Fisher Exact Probability Test. The analyses indicated that the occurrence of skeletal remains in recent sediments was independent of whether or not the reef had suffered a recent outbreak. Moran, Reichelt & Bradbury (1986) proposed from these results that it was erroneous to infer the occurrence of outbreaks in the past from similar debris in much older sediments. They concluded that while Frankel's data may demonstrate that *A. planci* had existed for a long time it did not prove that outbreaks of this animal had occurred in the geological past.

Randall (1972) has criticized the idea that outbreaks of starfish are natural phenomena which may occur regularly or periodically. He argued that the levels of coral community structure on the Great Barrier Reef and other reefs in the Indo-Pacific such as Guam could never have been attained if starfish outbreaks occurred regularly. Chesher (1969a) also adopted this line of reasoning suggesting that it was improbable that outbreaks had taken place on Guam over the last 200 years. Randall (1972) further criticized the notion that outbreaks are cyclical or periodic events on the basis that if they had occurred repeatedly over the years then reefs should be composed primarily of species that are least preferred by *A. planci* (e.g. *Porites* spp.). He felt that this was not the case on many reefs. The arguments raised by Randall (1972) are themselves open to question as they assume that outbreaks in the past were similar in duration and intensity to those recorded recently. At present there is no evidence to indicate that this is correct. Also, the latter criticism by Randall is based on the assumption that past outbreaks have occurred at relatively short intervals. Recent information has indicated that coral cover may regenerate to original levels within 10–15 years and that preferred corals such as *Acropora* spp. may tend to dominate these developing communities (see p. 447).

From surveys carried out in the South Pacific, Weber & Woodhead (1970) stated that *Acanthaster planci* was more common on reefs than is generally believed. This notion has been used by Dana & Newman (1972) and Dana, Newman & Fager (1972) to form the basis of the adult aggregation hypothesis (Potts, 1981). These authors considered that primary outbreaks originated when adult starfish are forced to aggregate after catastrophic events such as severe storms. The reasoning is that *A. planci* is normally common (but not necessarily obvious, visually) on reefs and under these conditions food is not a limiting factor. When large areas of coral are destroyed during tropical storms individuals aggregate in areas which have not been destroyed and where a large source of food is available. Mass mortality of corals during these conditions was thought to be a result of mechanical damage, sedimentation and freshwater input. Dana *et al.* (1972) used data from surveys carried out in Micronesia (Chesher, 1969a) to substantiate this hypothesis. They classified this information according to habitat type and starfish abundance. In doing so it was discovered, despite variability in the data, that the largest numbers of *A. planci* occurred on the leeward side of exposed reefs. Dana *et al.* (1972) postulated that these protected areas would be most susceptible to the formation of starfish aggregations as they often had an abundance of corals and supported a relatively large number of scattered starfish. They also were able to show from the survey data that the abundance of starfish in these areas (from 0.5–1.0

starfish per 100 m²) would be sufficient to cause the largest aggregations seen in Guam. In conjunction with these analyses Dana *et al.* (1972) showed that there was a positive correlation between the occurrence of typhoons and cyclones and the formation of outbreaks in Guam and the Great Barrier Reef.

This hypothesis is appealing since it can account for the fact that outbreaks initially appear to be composed of adults. Despite this however, the hypothesis has received little attention in the scientific literature. Potts (1981) suggested that it was one of the simplest hypotheses that had been put forward to account for the occurrence of outbreaks. While certain features recommend it, it also suffers several shortcomings. Although Dana & Newman (1972) and Dana *et al.* (1972) maintained that *A. planci* is generally common on reefs others have suggested that it is normally a rare animal (Pearson, 1975b; Endean, 1977). Potts (1981) considered that these authors may have under-estimated the true abundance of starfish under 'normal' conditions as they were derived from surveys that were carried out in relatively shallow water. He referred to data which showed that *A. planci* may also be found in deep water and thus considered that the surveys of Pearson (1975b) and Endean (1977) may have only sampled part of the habitat of this starfish. This debate is unresolved as there is little information on the abundance of starfish in deep water beyond the slope of reefs. A logical inconsistency in the aggregation hypothesis is that if an appreciable proportion of starfish is located in deeper water it is not exactly clear why these animals should aggregate as it is unlikely that these habitats would be as greatly affected by the types of disturbances mentioned by Dana *et al.* (1972). A further problem is encountered when trying to ascertain whether the abundances of starfish observed in primary outbreaks could have arisen from a dispersed normal population which has been forced to aggregate. Dana *et al.* (1972) maintained that the outbreak at Guam, which was estimated to comprise approximately 38 000 starfish, could have developed this way. On the other hand, it is much more difficult to believe that the supposed primary outbreak at Miyako Island in 1957 (Yamazato & Kiyan, 1973), which contained at least 220 000 starfish, could have arisen as a result of the aggregation of a normal population of dispersed individuals.

Apart from this, the adult aggregation hypothesis has been questioned by Pearson (1975b) who argued that these disturbances need not necessarily cause the mass mortality of corals and that large areas of coral may survive. This argument was based on observations he had made at a reef off Townsville which had recently suffered the effects of a major cyclone. Potts (1981) suggested that these observations did not invalidate Dana *et al.*'s (1972) hypothesis as it required only that intense coral mortality be confined to a localized area. This argument is somewhat pedantic as the term "localized area" may be defined in several different ways depending on the size of the reef. For an aggregation of starfish to take place in the manner suggested by Dana *et al.* (1972) the mortality of corals would have to occur over a large area. Newman & Dana (1974) have suggested that this hypothesis could be tested empirically by limiting the amount of food available (either by removing coral or increasing starfish numbers) and observing whether the starfish move into areas with abundant coral.

Two other hypotheses have been proposed that suggest that outbreaks are a consequence of natural processes. One of them proposes that the recruitment of larvae of *A. planci* is enhanced during times of favourable environmental conditions and can be termed the larval recruitment hypothesis. This hypothesis was based on the results from laboratory experiments, which showed that the survival of larvae is improved under conditions of lowered salinity (about 30‰) and higher temperature (around 28 °C) (Lucas, 1973, 1975). Lucas (1972) proposed that the survival rate of larvae may be increased if these conditions occurred in the field. From this he hypothesized that a slight alteration in the survival rate of larvae could lead to large increases in the number of individuals that settle and this may result in population outbreaks of *A. planci* in later years. Pearson (1975b) demonstrated that these sorts of conditions may occur within 50 km of the North Australian coast (between Ingham and Mossman). Like Dana *et al.* (1972) and Nishihira & Yamazato (1974), he considered that these conditions may be associated with periods of heavy run-off as a large proportion of rivers were located in this region. He proposed that there would be a greater chance of outbreaks occurring if there was a higher survival of larvae. Pearson (1975b) suggested that high larval survival may not always occur after times of flood as the right rainfall conditions would need to be combined with periods of light wind (which would prevent the water layers from being mixed) and the availability of large areas of suitable substratum.

In this hypothesis natural processes are seen to be the primary cause of starfish outbreaks. It also allows for the fact that the frequency of occurrence of these processes, and thus outbreaks, may have been increased indirectly by man's activities (Dana, 1970). For example, the development of land may have increased the amount of run-off into the sea thus leading to more frequent starfish outbreaks. With this in mind it has been pointed out that nearly all of the outbreaks which have occurred in the Indo-Pacific region have occurred on reefs near high islands or mainland continents (Tsuda, 1971; Pearson, 1975b).

Another hypothesis also explains the occurrence of outbreaks in terms of natural processes. This hypothesis, developed by Birkeland (1982), has several features in common with that of the larval recruitment hypothesis. It also emphasizes the importance of run-off in creating outbreaks of starfish and, therefore, can be referred to as the terrestrial run-off hypothesis. While Pearson (1975b) stressed that run-off from landmasses created environmental conditions (decreased salinity and increased temperature) which enhanced larval survival, the terrestrial run-off hypothesis suggested that the nutrients in run-off from high islands and continental land masses caused phytoplankton blooms which acted as a food source for larvae, thus promoting their survival. This is also based on results which have emanated from studies conducted in the laboratory. The findings of Lucas (1982) suggested that food availability was important in determining the survival of larvae (see p. 397). Birkeland (1982) has adopted this view and made it the central theme of his hypothesis. Implicit in it is the belief that under normal conditions the survival of larvae is low due to a lack of food. The high larval mortality under these conditions may be the result of starvation or predation (see p. 397). During times when there is sufficient food, such

as when phytoplankton blooms occur, the survival of larvae is enhanced. Like Lucas (1972), Birkeland (1982) suggested that a small percentage increase in the survival of larvae could lead to a great increase in the number of adults on reefs.

By correlating rainfall data with information on outbreaks he showed that outbreaks of *A. planci* follow some three years after periods of heavy rainfall (*i.e.* >100 cm in three months or 30 cm in 24 h) which themselves have followed times of drought (*i.e.* <25 cm in four months). From these analyses he found that outbreaks did not occur after "dry" typhoons (which produce little rain) but only followed from "wet" typhoons. He also showed that they tended to take place around high islands but not coral atolls. On the basis of this information he successfully predicted an outbreak of starfish at Saipan in 1981.

Birkeland (1982) pointed out that one of the main advantages of his hypothesis was that it could account for the sudden appearance of large numbers of starfish which he considered characteristic of outbreaks. He stated that this feature indicated that outbreaks arise from periods of successful recruitment and not from a decrease in predator pressure, which he considered would result in the gradual build-up of individuals over a number of years. In addition, he maintained that since outbreaks occurred at so many localities and were composed of such large numbers of starfish it could be implied that the increased survival of larvae was the main factor involved.

While the larval recruitment and terrestrial run-off hypotheses have much to commend them they fail to address several points. For example, it is assumed for outbreaks to arise that spawning must have been successful in terms of the proportion of eggs fertilized. The hypotheses do not explain how large numbers of larvae are produced from a population which under normal conditions would be dispersed. It is not known what percentage of eggs are fertilized in the field when adults are dispersed. Presumably, the extent to which fertilization occurs depends on adult density although perhaps a threshold level of individuals is needed before large numbers of larvae are produced. It is possible that adults in a normal population aggregate during spawning due to biochemical means; few such aggregations have, however, been observed in the field.

The validity of these two hypotheses has also been questioned on the grounds that they require the synchronization of a number of different and highly variable processes (Potts, 1981). They require that the spawning of adults occurs within a short time after the onset of heavy run-off. Birkeland (1982) maintained that spawning occurred at the start of the wet season on either side of the equator at a time when phytoplankton blooms are most likely to arise. The synchronization of these two processes presupposes that the bloom conditions remain intact and undispersed for at least several weeks. Similarly, prolonged conditions of reduced salinity are required under the larval recruitment hypothesis. In addition, for outbreaks to occur on isolated reefs (such as in Micronesia) during periods of bloom conditions or optimal physical conditions then a favourable hydrodynamic regime must prevail so that larvae are not dispersed away from these areas.

It can be seen that synchronization of a number of variable events is assumed for both hypotheses. Potts (1981) stressed that there was no direct evidence to support the larval recruitment hypothesis and that no outbreak

of juveniles has been recorded in the field. This criticism may also be levelled at the terrestrial run-off hypothesis as both hypotheses suggest that primary outbreaks will arise from the settlement of high densities of larvae. While it is true that no such outbreaks (apart from those mentioned earlier) of juveniles have ever been observed this may not be a valid criticism as little is known about where larvae settle on reefs. If they settled in deep water off, or at the base of reef slopes then it is possible that high densities of juveniles may go unnoticed until they become adults and capable of moving and feeding over large distances.

Cameron (1977) and Cameron & Endean (1982) have also raised doubts about the validity of the terrestrial run-off hypothesis in explaining the occurrence of outbreaks in various parts of the Indo-Pacific region. They argued that the life history of *A. planci* was not unique among other asteroids. For example, they compared its life history with that of *Culcita* sp. and found that both starfish were carnivores, had similar distributions and larval biologies, and were large in size. In view of this similarity they stated that the terrestrial run-off hypothesis failed to explain why animals with similar life histories to *Acanthaster planci* did not outbreak. This question will remain unanswered until more detailed data are obtained on the larval ecology of these starfish.

While the hypothesis proposed by Birkeland (1982) may hold for isolated areas in Micronesia and the south Pacific where primary outbreaks can be presumed with some degree of certainty, there are no data as yet to indicate that it can be applied to outbreaks on the Great Barrier Reef. The data presented by Birkeland (1982) for this area are at variance with the pattern of outbreaks recorded for that particular time. These data indicated that outbreaks of *A. planci* occurred in 1962 on reefs along the Queensland coast between Townsville and Bowen. This is incorrect as outbreaks were not reported in this area until the early 1970s. By 1962 they had only just been reported at Green Island (Pearson & Endean, 1969) (see p. 432). Another inconsistency is that the outbreaks which occurred in this area were correlated with an intense cyclone (the third most severe on record) which crossed the coast in 1959. According to the terrestrial run-off hypothesis outbreaks take place after a period of high rainfall which itself has been preceded by a period of dry weather. The date (1959) given by Birkeland (1982) is inconsistent with this explanation since according to Dana *et al.* (1972) a severe cyclone had also affected the area in question in 1958. Dana *et al.* also mentioned that increased cyclonic activity was experienced along much of the Queensland coast during the period from 1958–1961. Clearly, more accurate data on past and present weather conditions and outbreaks are needed before it can be determined whether the terrestrial run-off hypothesis can be applied to the Great Barrier Reef system.

The idea that outbreaks are unnatural phenomena is mainly based on the premise that they have not occurred in the past. Another underlying assumption is that coral reefs are complex systems that are biologically stable and predictable. It is postulated that the inertia of these systems prevents species or groups of species from undergoing marked changes in their population structures. The homeostatic mechanisms responsible for this reside in a system that is highly diverse and dominated by co-evolved relationships among species.

Cameron (1977) and Cameron & Endean (1982) considered that *A. planci* was rare, large in size, relatively long-lived, morphologically and chemically specialized for feeding and defence, and had few parasites. Like Moore (1978), they based their conclusions on the life history and ecology of the animal. They, however, regarded it as a rare and specialized carnivore and not an opportunistic species. From a theoretical point of view they stated that outbreaks of this starfish were a unique event within complex systems such as coral reefs and, therefore, were indicative of a novel sort of perturbation. Although the ideas of Moore (1978) and Cameron & Endean (1982) are divergent they are important as they represent the first attempts to link present concepts in theoretical ecology with information on the *Acanthaster* phenomenon. They both suffer from inadequate data. For example, Cameron (1977) and Cameron & Endean (1982) presumed that *A. planci* was long-lived although there are no data on the longevity of starfish in the field. Also, they stated that *A. planci* had very few parasites although recently it has been suggested that they may suffer from a bacterial infection (see p. 419).

Cameron & Endean (1982) have emphasized that outbreaks of *A. planci* represent a novel event in complex tropical reef systems. Birkeland (1982, 1983) disagreed with this view and has proposed that certain animal populations apart from *A. planci* may fluctuate widely in their abundance. He gave the examples of *Diadema setosum* and *Echinothrix diadema* which were recorded in large numbers at Guam in 1977. He further stated that there were many species of planktonic larvae and tropical invertebrates (e.g. insects) whose populations were characterized by large fluctuations. He stated that there was no empirical basis for suggesting that coral reefs were predictable, stable systems. This view was also supported by Sale (1980) who concluded that the available evidence showed that coral reef fish communities were predominantly unstable and suffered from large fluctuations in recruitment.

In general, hypotheses which have emphasized that outbreaks are unique or unnatural phenomena have explained their occurrence in terms of man-induced perturbations. It has been pointed out that all major outbreaks have occurred near centres of human populations (Chesher, 1969a). Chesher (1969a) proposed that increases in blasting and dredging in Micronesia may have been responsible for creating large areas of clear space which would favour the settlement of larvae, thus increasing their survival. He suggested that larval mortality was normally high as a result of predation by benthic organisms such as corals. The destruction of large areas of reef by these activities was thought to enhance the survival of larvae by reducing predation and to provide an abundance of suitable substrata for settlement. Chesher (1969a) presumed that this would perhaps allow more starfish to settle and that these centres of settlement would in turn develop into "seed" populations. In support of this hypothesis he gave examples of several areas in Micronesia, particularly Guam, where outbreaks of starfish had occurred after dredging and blasting had been undertaken. This hypothesis has been criticized for a number of reasons. First, Endean (1977) maintained that there was insufficient evidence to support this hypothesis. Secondly, Branham (1973) stated that it did not account for why outbreaks occurred during the same period throughout the Indo-Pacific. Thirdly, it

has been pointed out by Randall (1972) that outbreaks of starfish have occurred on reefs where such activities had never been reported. Finally, the hypothesis does not explain why outbreaks of starfish were not recorded during or immediately after the Second World War on many reefs in Micronesia which experienced extensive blasting, dredging and bombing (Endean, 1977).

Nishihiro & Yamazato (1974) found, on the island of Okinawa, that starfish outbreaks appeared to occur more intensively on reefs which were affected by human activities. They did not, however, suggest a reason for this. Hypotheses have been put forward by Fischer (1969) and Randall (1972) which link man's activities with the occurrence of outbreaks. They stem from the observation that all major starfish aggregations have occurred near populated areas. In both hypotheses it is proposed that the increased input of chemical pollutants into the sea by man has been responsible for reducing the predators of larval and adult crown-of-thorns starfish. This in turn has allowed far greater numbers of starfish, particularly larvae, to survive. There is very little evidence to support this hypothesis or indeed the notion that coral reefs are being polluted by chemicals such as pesticides. The results of a study by Tranter (1971) showed that the tissues of three animals (*Acanthaster*, *Linckia*, and *Tridacna*), collected from sites near human populations on the Great Barrier Reef, contained only very low amounts of chlorinated hydrocarbons. He concluded from this that they were not greatly polluted by pesticides. A study reported by Haysom (1972) also indicated that there was little evidence to indicate that chemical pollutants were in abnormally high concentrations in waters of the Great Barrier Reef. No significant difference was found in the pesticide levels of oysters from several different locations. Further studies by McCloskey & Deubert (1972) found no correlation between starfish abundance and organochlorine concentrations in the gonads of starfish from areas within the Great Barrier Reef, Micronesia, and Hawaii. They also discovered that not all the highest levels of these pesticides came from starfish in areas close to human populations.

Of all the hypotheses which focus on man-induced causes that proposed by Endean (1969) has received the greatest attention in the scientific literature. This hypothesis emphasizes that outbreaks of *Acanthaster planci* are unique events which arise because man has removed the predators of this starfish. Thus it can be termed the predator removal hypothesis (Potts, 1981). Initially, the major predator controlling starfish numbers on the reef was thought to be the giant triton (*Charonia tritonis*) (Endean, 1969). Endean (1973a) stated that this animal was a predator of large juvenile and small adult starfish, a fact which had been well documented in the scientific literature. Large adults were not thought to experience heavy predation because of their greater defensive capabilities (*i.e.* size, toxicity of spines, behaviour) and because they had been observed to escape from attack by *C. tritonis* and regenerate any damaged tissue (Chesher, 1969a). This is indicated in the field by the high percentage of starfish which have been found to have missing or regenerating arms (see Table VII, p. 418). Small starfish presumably would not suffer high levels of predation because of their size and ability to inhabit small crevices and spaces which could not be invaded by *C. tritonis* (Chesher, 1969a). Endean (1973a) claimed that

collection of *C. tritonis* by man had occurred increasingly since the end of the Second World War and had resulted in an increase of starfish on some reefs. It was proposed that this build-up of adult starfish to a threshold level culminated in the production of large numbers of larvae which drifted to other reefs causing primary outbreaks. Further support for this hypothesis comes from Fagoonee (1985a) who reported that *Acanthaster planci* had greatly increased in numbers at Mauritius, at a time when the abundance of *Charonia tritonis* had decreased due to its collection by man.

Birkeland (1982) has disagreed with this hypothesis on the grounds that the mechanism proposed by Endean (1973a) would lead to a gradual increase in starfish numbers over several years whereas observations in the field indicate that outbreaks build-up very suddenly. The validity of the predator removal hypothesis also has been questioned by Chesher (1969a) and Vine (1970) who claimed that *C. tritonis* is normally rare on reefs and, therefore, could not be responsible for controlling the abundance of juvenile and adult starfish. This view has received additional support since experiments with caged starfish showed that *C. tritonis* may eat less than one starfish per week and that it prefers to consume other species (e.g. *Linckia* sp.) if given a choice (Chesher, 1969a; Pearson & Endean, 1969). Potts (1981) has provided a detailed summary of the results of these studies. To date, no experiments have been conducted to determine the extent to which *C. tritonis* preys on juvenile and adult starfish in the field.

In more recent years Endean (1977, 1982) has extended this hypothesis to include the effects of fish predators such as the groper *Promicrops lanceolatus*. Other species that have been observed to feed on *Acanthaster planci* (e.g. *Balistoides viridescens*, *Pseudobalistes flavimarginatus*, and *Arothron hispidus*) (Ormond & Campbell, 1974) were not included in the hypothesis as it was doubted whether they were important predators on the Great Barrier Reef. This extended version of the predator removal hypothesis stressed that *Charonia tritonis* was a major predator of large juvenile and small adult starfish whereas *Promicrops lanceolatus* preyed on juvenile *Acanthaster planci*. Endean (1969, 1974, 1977) considered it unlikely that starfish abundance would be controlled by the predation of eggs and larvae for two reasons. First, this type of predation would not be specific to *A. planci* and, therefore, should lead to population increases in other similar animals. The fish *Abudefduf curacao* was observed to feed on eggs of *Acanthaster planci* (Pearson & Endean, 1969), although Endean (1974) pointed out that there was no evidence to indicate that there had been a decline in the predation of starfish eggs in recent years. Secondly, experiments by Howden *et al.* (1975) and Lucas (1975) have shown that the eggs and larvae may not be eaten by fish because they contain toxic saponins. Endean (1982) claimed that the collection of triton shells and overfishing of some reefs may have been responsible for recent starfish outbreaks. He maintained that this hypothesis correlated well with the history of starfish outbreaks on the Great Barrier Reef.

Rowe & Vail (1984a), in reviewing current knowledge of the *Acanthaster* phenomenon stated that the predator removal hypothesis was no longer accepted by most scientists. This comment may be true but it fails to point out that scientists in general are not in a position to be able to make an objective decision concerning its validity on the grounds that very little is

known about predation in general. This is a feature of each of the hypotheses presented in this section. Clearly, an extensive series of field experiments is needed in order to generate a more informed debate of this issue. Recently, it has been recommended that modelling studies be undertaken to test hypotheses which incorporate man-induced triggers (Crown of Thorns Starfish Advisory Committee, 1985) but even these studies require more empirical information on factors influencing the distribution and abundance of *A. planci* than is at present available.

The predator removal hypothesis, like all hypotheses has weaknesses. Potts (1981) regarded it as "the least satisfactory model" on the grounds that it relied on some invalid assumptions and there was little before and after information on triton numbers which would allow the hypothesis to be tested. He disputed the notion that *Charonia tritonis* was a "specialist" predator of *Acanthaster planci* and that it was capable of controlling the numbers of juvenile and adult starfish. Chesher (1969a) has raised some further doubts concerning this hypothesis particularly in relation to its application to outbreaks in other parts of the Indo-Pacific. He considered that it was possible that the collection of tritons had lead to outbreaks of starfish on some reefs in Micronesia. He, however, made the point that outbreaks occurred on some isolated reefs in this region (e.g. Ponape, Tinian, Ant, and Truk) where fishing and shell collecting were unlikely to have been carried out. Conversely, he suggested that outbreaks of starfish were not recorded on several reefs (e.g. Ifalik, Woleai, Kapingamarangi) where these activities were intensively conducted.

Two other features of the predator removal hypothesis require explanation. First, Endean (1974) stated that the collection of triton shells had occurred until 1969 when it became a protected species. Almost 16 years have elapsed since then and it is presumed that the triton populations have begun to recover. What is not readily apparent is why outbreaks are at present occurring on the Great Barrier Reef when this animal has been protected for so many years? Secondly, it is not known whether the progressive removal of tritons over a number of years would lead to a gradual build-up in starfish numbers, as suggested by Birkeland (1982), or whether it would cause the rapid appearance of outbreaks. If it produced a gradual increase in starfish abundance then most likely this would have been manifested on a number of reefs on the Great Barrier Reef as shell collecting and fishing have been carried out over a large part of this region. This facet of the hypothesis should be testable using population models of the phenomenon.

This completes a discussion of the main hypotheses which have been raised to account for the occurrence of starfish outbreaks. Other mechanisms have been postulated, such as genetic mutations of *A. planci* (Antonius, 1971), but there is no evidence to support them.

CAUSE OR CAUSES?

It should be recognized that the hypotheses discussed above have some basis in fact or offer apparently plausible reasons for the occurrence of outbreaks. As there are, however, inconsistencies within each, no one hypothesis fully explains the occurrence of outbreaks of *A. planci*. This is

for several reasons. First, many are based on a correlative approach and consequently they do not demonstrate true cause and effect. Kendall & Stuart (1979) have discussed the problems involved in establishing causation by studying the interdependence of two variables. Secondly, because so little is known about *A. planci* in the field all the hypotheses suffer, to varying extents, from a lack of supporting evidence. Thirdly, in some instances they are based on evidence which is equivocal and can be interpreted in a number of different ways. Finally, some stem from information which has been derived from outbreaks in specific areas and, therefore, inconsistencies emerge when they are extrapolated to account for the global pattern of outbreaks. Perhaps a criticism which may be levelled at all hypotheses is that they tend to be overly simplistic and seek to explain the occurrence of outbreaks in terms of a single (global) process (*e.g.* predation, terrestrial run-off, pollution). Randall (1972) and Endean (1977) suggested that the probability of outbreaks occurring concurrently in different reefal areas, separated by large distances, was low and that this was indicative of a single controlling factor. No doubt there is some truth to this statement as there are a number of similarities among the outbreaks that have occurred throughout the Indo-Pacific. These are given below.

- (1) All major outbreaks in the world have occurred near landmasses (*e.g.* Great Barrier Reef, Ryukyu Islands, Micronesia, Fiji, Samoa, Hawaii, and Tahiti). Exceptions to this are the outbreaks that have been recorded on Elizabeth and Middleton reefs in the Tasman Sea. These may, however, have resulted from an influx of larvae from the Great Barrier Reef.
- (2) Most outbreaks appear to be synchronized, having occurred over the same general period (*i.e.* 1960s–1970s). Of late, outbreaks have once again arisen in several areas at about the same time (*i.e.* late 1970s–1980s). Examples of these are the Great Barrier Reef, Guam, Palau, Saipan, and Fiji.
- (3) Several reefs appear to have suffered extensive outbreaks on both occasions (*e.g.* Great Barrier Reef, Fiji, Guam and Palau).

While there are certain similarities among outbreaks that have occurred in the Indo-Pacific there is no reason to suppose that this is because they each originated as the result of the same single process (Weber & Woodhead, 1970). Indeed the fact that no one hypothesis can account fully for their occurrence suggests that a number of processes may be involved. The information presented earlier in this paper indicates that outbreaks may be caused by a complex interaction of factors which are poorly understood. Perhaps a more accurate explanation of the global occurrence of outbreaks may be achieved by considering the effects of a number of processes which may vary in their importance and their relationship with each other in different areas. To date, no hypothesis has incorporated this type of approach probably because there is so much that is not known about this starfish.

It is worth pondering whether our understanding of the *Acanthaster* phenomenon is hamstrung because there is a tendency to rely on hypotheses which may provide simplistic answers to what may be a far more complex question?

Perhaps the real answer may lie in a collage of the main hypotheses proposed earlier. A similar suggestion was also made by Potts (1981). It is possible that adults may aggregate under natural conditions as proposed by Dana *et al.* (1972). If the spawning of these adults coincided with times of heavy run-off, high food abundances (Birkeland, 1982) and optimal physical conditions (Pearson, 1975b), then this may lead to the increased survival of larvae. The settlement of large numbers of larvae and the establishment of dense aggregations of juveniles may occur provided predation is not extensive (Endean, 1982). This hypothetical example still allows for the possibility that outbreaks may be man-induced or that their frequency of occurrence has been increased by man. Answers to this question may involve a much more intensive study of each process and the relationships between them in order to determine the critical pathways in the system.

Of course, this explanation may also be inadequate, but one must be alert to the possibility that this phenomenon may not be explained easily and that to trust to one hypothesis is akin to putting on blinkers. In the future as more is known about *A. planci*, particularly its ecology, there must be a willingness to modify and extend hypotheses. Otherwise our knowledge of this phenomenon may stagnate and will revolve around a debate of the same ideas and issues; this has happened already to a certain extent. Only in this way may we be able to appreciate more fully the *Acanthaster* phenomenon. Obviously with the difficulties faced by scientists in undertaking studies in the field several aspects of this animal's biology may never be fully comprehended. Hence Bradbury, Done *et al.*'s (1985) warning that more research may not lead to a complete understanding of the phenomenon. The success of future research may well depend on addressing the right research questions at the correct time. For this to happen it is imperative in dealing with this episodic animal that the availability of funds, the formulation of research questions, and the occurrence of outbreaks be synchronized. Unfortunately this has not happened to date, despite the large number of committees and governmental bodies that have been formed to look into this problem (*e.g.* in Australia alone—Walsh *et al.*, 1970, 1971, 1976; Advisory Committee on the Crown of Thorns Starfish, 1980; Crown of Thorns Starfish Advisory Committee, 1985; Milton, 1985).

In conclusion, future research on the *Acanthaster* phenomenon is important for several reasons. First, it will extend our knowledge of outbreaks of invertebrate populations. Secondly, and just as important, it offers scientists the unique opportunity to obtain a greater understanding of coral reefs and the processes that are important in structuring them. Finally, it will help scientists to decide whether the phenomenon is a problem, in the sense that it may be causing irreparable and unnatural changes to many of the world's coral reefs.¹

¹At the end of 1985 the Australian Government allocated \$971,000 to the Great Barrier Reef Marine Park Authority to initiate what is anticipated will be a four-year research programme on the crown-of-thorns starfish.

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ANNOTATED BIBLIOGRAPHY

The present edition takes into account those works which have been published up until February 1988. This document includes an updated and extended set of annotations which hopefully will be of greater assistance to those who wish to track down certain references pertaining to the *Acanthaster* phenomenon. In general, most papers have been classified by a set of annotations rather than just one.

As the number of references on *Acanthaster* continues to grow the bibliography will begin to take on an entirely new structure to that which was used for the review. However, those references that formed the basis of the review will always be a subset of this work (and so can be readily found). Like the previous edition, some references have not been included in this document; notably those of a more popular nature which fail to give much useful information or are too general. Once again, unpublished works have been included in this edition but only if they are readily obtainable (this has been noted in the text).

Several of the references included had no stated authorship. These references have been listed in alphabetical sequence by the first word of the item's title.

A new feature of this bibliography is the addition of an Appendix which contains references to works which at the time of writing had not been read (and hence could not be given an annotation) as they were completely in a foreign language or they could not be obtained. These references have been included here for those who require the most up-to-date information possible and who have the necessary resources at their disposal to track this information down. In future editions it is likely that a proportion of these references will find their way into the main body of the document.

Key to Annotations

The following classifications have been used as a means to best describe each paper in this bibliography and are given in square brackets at the end of the citation. It should be noted that more than one annotation has been used to describe papers which cover several topics.

1. Popular article
2. Review:
 - (a) Extensive
 - (b) General
 - (c) Specific
3. Distribution and abundance of *Acanthaster*/surveys
4. *Acanthaster* biology:
 - (a) Morphology
 - (b) Toxicity
 - (c) Systematics/genetics
 - (d) Reproduction/larvae
 - (e) Life cycle
 - (f) Dispersal/recruitment
 - (g) Growth and development
 - (h) Feeding
 - (i) Movement
 - (j) Physiology
 - (k) Metabolism
5. *Acanthaster* ecology:
 - (a) Habitat
 - (b) Population dynamics
 - (c) Symbionts/parasites
 - (d) Predation
6. Biochemical aspects of *Acanthaster*:
 - (a) Feeding
 - (b) Toxicity
 - (c) Other
7. Methodology/techniques for study of *Acanthaster*:
 - (a) Surveys
 - (b) Controls
 - (c) Laboratory
 - (d) Field
8. *Acanthaster* control programs

9. Cause(s) of *Acanthaster* outbreaks:
 - (a) Evidence for or against
 - (b) Hypotheses
10. Models of the *Acanthaster* phenomenon:
 - (a) General/descriptive
 - (b) Mathematical/theoretical
 - (c) Quantitative
 - (d) Qualitative
 - (e) Biological/predation
 - (f) Spatial
 - (g) Temporal
 - (h) Control
11. Effects of *Acanthaster* outbreaks on coral communities:
 - (a) Destruction
 - (b) Recovery
 - (c) Symbionts/commensals
12. Effects of *Acanthaster* outbreaks on other reefal communities:
 - (a) Destruction
 - (b) Recovery
13. *Acanthaster* Research:
 - (a) Status of/knowledge gained
 - (b) Future
14. Critique
15. Historical/sociological/political

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